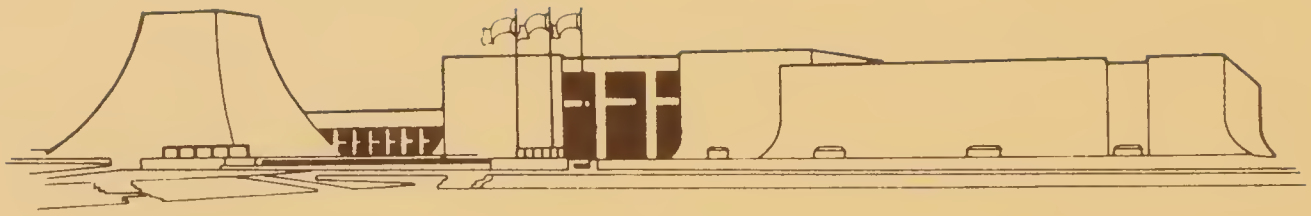

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Contents

## Introduction

The long-eared myotis, *Myotis evotis* (H. Allen, 1864), is one of the least-studied members of the genus in North America. Only recently has the available information concerning its distribution, habitat, reproductive biology, and natural history been summarized (Manning and Jones, 1989). From a systematic point of view, two subspecies were recognized at the onset of this study, *M. e. evotis* of the mountainous regions and High Plains of the western United States and adjacent southwestern Canada, southward into Baja California Sur (on the basis of a single specimen from Comondú), and *M. e. pacificus* from coastal regions of the Pacific Northwest (Hall, 1981). Additionally, a closely related species, *Myotis milleri*, occurs in the Sierra San Pedro Mártir in northern Baja California. There is little doubt that the *M. evotis* complex is in need of systematic revision (Honacki *et al.*, 1982; Reduker *et al.*, 1983). In the last review of the genus *Myotis* (Miller and Allen, 1928), only 122 specimens of the long-eared myotis were examined, of which 42 were assigned to *M. e. pacificus* and 80 were identified as *M. e. evotis*. A morphometric study of this bat from throughout its range was undertaken to document geographic and nongeographic variation in this species, and thus provide the basis for an appropriate systematic arrangement of intraspecific populations.

## Taxonomic History

The long-eared myotis has had a tortuous taxonomic history, especially with regard to populations on the West Coast. Harrison Allen (1864) originally named this species as *Vespertilio evotis*. No holotype was designated, the description having been based on a total of 13 specimens subsequently recognized as constituting a composite series (for example, specimens from Baja California now are known to represent *M. californicus*) from the following locations (number of specimens from each locality in parentheses): "Upper Missouri" (3); Puget Sound (3); east of Colville, northeastern Washington (2); Monterey, California (1); Cape St. Lucus, Baja California Sur (2); mountains of New Mexico (1); and one specimen without locality data. The species "appears to be comparatively common along the Pacific coast from Puget Sound to Lower California" (H. Allen,1864:49).

Thirty years later, in his revised monograph of bats of North America, H. Allen (1894) reduced the long-eared myotis to subspecific status under the name *Vespertilio albescens evotis*. He wrote (p. 89) that "Herein is embraced a group of forms which find expression in the highlands of Montana, Colorado, and Arizona, though sparsely found in California." In the same publication, Allen made specific reference to a specimen from Easton, Washington, as follows: " This is the typical *V. evotis* of the monograph. It would certainly be a distinct species if the southern form did not show tendencies toward *V. albescens*." Included in specimens examined was yet another undescribed species (*Myotis thysanodes*) from Old Fort

Tejon, California. As in the original description, no holotype or type localtiy was mentioned for *evotis*.

J. A. Allen (1896) described a new species of long-eared myotis, *Vespertilio chrysonotus*, based on a single specimen from the Kinney Ranch, Wyoming. "It differs from Dulzura [California] specimens of *V. evotis* in its golden-buff color, much longer forearm, and much shorter [admittedly damaged] tail. It evidently belongs to the *evotis* group, of which further material may show it to be merely a well marked subspecies" (J. A. Allen, 1896:240).

In his revision of North American vespertilionid bats, G. S. Miller (1897) was the first to apply the name *Myotis evotis* to the long-eared myotis. He placed *chrysonotus* as a synonym of *evotis*. Concerning the type locality of this species, he wrote (pp. 77–78): "In the original description specimens are mentioned from the upper Missouri River, and the Pacific coast from Puget Sound to Cape St. Lucas. Monterey, Cal. (one of the localities given), may be selected as the type locality." He had already done this, however, on an earlier page (p. 40), because there he listed the type locality of *Myotis evotis* (H. Allen) as "Monterey, California." Miller's intent, under the first revisor principle, in fixing the type locality of *M. evotis* is clear. Subsequent attempts to support or alter this decision are discussed beyond and in the account of *M. e. evotis*.

The total number of specimens examined by Miller (1897) was 32, of which at least one (from Perote, Veracruz), was of an undescribed species of long-eared bat (*Myotis auriculus*). Of *chrysonotus*, he wrote that "in color the type of *chrysonotus* is a barely perceptible shade yellower than skins of *evotis* from San Bernardino mountains, California, and Vermejo River, New Mexico, but the difference is wholly inconsequential" (Miller, 1897:80). Miller and Rehn (1901) followed Miller (1897) in listing the type locality of *evotis* as Monterey, Monterey Co., California.

Another long-eared bat, *Myotis milleri*, the description of which was based on two specimens from La Grulla, 8000 feet, San Pedro Mártir Mountains, Baja California, México, was named by D. G. Elliott. He noted that "from *M. evotis*, to which it is probably nearest allied, it is at once distinquishable by its different color and larger ears" (Elliott, 1903:173).

In 1909, E. W. Nelson and E. A. Goldman described yet another long-eared taxon, *Myotis micronyx*, based on a single specimen from Comondú, Baja California Sur. They (1909:28) described *micronyx* as follows: "Much like *M. evotis*, but slightly smaller, with proportionally much smaller ears, thumb and claws; free border of interfemoral membrane indistinctly ciliate as in *evotis*. Fur of upperparts, including middle of face, light golden cinnamon; sides of face thinly covered with dusky hairs; underparts gray, slightly tinged with buff. [Skull is] similar to *evotis*, but narrower; braincase higher, more inflated anteriorly, arching more abruptly from rostrum; palate narrower behind molars; bullae smaller. From that of *milleri* the skull differs in the same characters as from *evotis*."

Miller (1912) again listed the type locality of *M. evotis* as Monterey, California. In a subsequent publication, however, Miller (1924) gave the type locality as "Puget Sound," citing H. Allen's (1894) statement regarding a specimen from Easton, Washington, as "typical *evotis*," and thus fixing the type locality. Easton, however, is east of the Cascade Range and not near Puget Sound. In the most recent revision of this genus, Miller and Allen (1928) inexplicably listed two different type localities for *M. evotis evotis*—"Near Colville, Wash." (p. 10), and "Puget Sound" (p. 114).

Also, in the same revision, they (1928:23) placed *M. micronyx* in synonymy with *M. evotis* because "apparently [it is] not distinguishable from *M. evotis chrysonotus*." They recognized two races of long-eared myotis, a dark-colored subspecies (*evotis*) of the Pacific coastal region of the Northwest, and a paler inland subspecies (*chrysonotus*) that occurred over the remainder of the known distribution, including (incorrectly, as later shown) much of México, south at least to Perote, Veracruz.

Dalquest (1943) presented arguments for accepting Miller's (1897) initial designation of Monterey, California, as the type locality for the nominate subspecies. Because bats occurring there are pale in color, Dalquest regarded them as representing *evotis*, thus leaving the dark coastal race without a name. He thus applied the subspecific name *evotis* (with *chrysonotus* as a synonym) to the pale-colored, mostly inland population, and proposed the name *Myotis evotis pacificus* for the dark coastal subspecies, with type locality near Yacolt, Clark Co., Washington.

The only other major taxonomic change that has contributed to an understanding of the distribution of the *M. evotis* group was the recognition of another big-eared species of myotis, *M. auriculus* (see Genoways and Jones, 1969) from the southwestern United States and México, both subspecies of which originally were named as races of *evotis* ( Baker and Stains, 1955; Hoffmeister and Krutzsch, 1955).

As noted by Miller and Allen (1928:113–114) a half century ago: "The series of skins available for study is not very extensive, as *Myotis evotis* appears to be nowhere a common bat. So far as it goes, the material indicates that the species is divided into two rather ill-defined geographic races, a darker typical form confined to the humid northwest coast region and a lighter form occupying the rest of the animal's range. That all of the lighter individuals represent a single geographic race appears to be highly improbable, but material now at hand is not sufficient to form the basis for satisfactory subdividing."

Specimens now available in museum collections are of sufficient number from across the known geographic distribution of the species to evaluate and analyze morphometric variation within *M. evotis*, which is the subject of this study.

## Natural History

Nowhere is the long-eared myotis an especially common bat. Most of the information relating to the biology and natural history of this species is, therefore, anecdotal. Recently, available data were summarized by Manning and Jones (1989) and much of the information in this chapter is drawn from that source.

### *Reproduction*

As in most other species of North American *Myotis*, female *M. evotis* typically bear young in late spring or early summer. Reproductive information compiled from specimen labels of 26 pregnant females examined from the months of May, June, and July indicate that each carried a single fetus. Minimum and maximum crown-rump lengths (mm) of fetuses, by month, are as follows: May ("tiny"–6); June (4–21); July (15–25). The earliest recorded date of pregnancy (female from Socorro County, New Mexico) is 13 May, whereas the latest record (female from Wallowa County, Oregon) is 26 July—crown-rump lengths, 3 and 19, respectively. Specimens identified as lactating were examined from the months of June, July, August, and September. Earliest available recorded date of capture for a lactating female is 28 June (Socorro County, New Mexico), whereas the latest is 9 September (Malheur County, Oregon). However, it is of note that a female was taken with young (no measurements recorded) on 24 June in San Luis Obispo County, California. One specimen label (female taken on 24 July in Union County, Oregon) had the following standard measurements for a male fetus: total length, 40; length of tail, 15; length of hind foot, 6; and length of ear, 9. Maser *et al.* (1981) provided the following measurements of neonates born on 15 and 16 July in Oregon: total length, 40 to 47 mm; weight, 1.08 to 1.36 grams, wingspan of one young was about 103 mm.

Ranges in length of testes (mm), by month, for 106 males from across the range of the species are as follows: May (2–4); June (2–4); July (2–6); August (2–7.5); September (1–4); October (abdominal, 3).

### *Pelage and Molt*

Juvenile pelage of *M. evotis* is shorter than adult pelage and has an overall "woolly" appearance. Individual hairs of the dorsum are more uniformly grayish, with less contrast between base and tip, whereas ventral hairs tend to be more whitish gray than tan-buff as seen in adults. Sample sizes available for my study were too small to allow direct comparisons of the precise timing and sequence of molt from across the entire range of the species. In general, juvenile pelage was present in some individuals until mid-to-late summer. After adult pelage is attained, a single seasonal molt occurs, usually in July and August. Comments on pelage color (red, green, and blue reflectance color measurements) and comparisons within and between samples are discussed in the accounts of subspecies.

### *Ecology*

*Myotis evotis* occurs throughout mountainous regions and adjacent areas of most of the western United States, southwestern Canada, and parts of Baja California, México. In most references in the literature, coniferous forests are mentioned as an important component of habitats in which these bats are found. Individuals frequently inhabit boreal areas at relatively high elevations. Some authors, however, have reported long-eared myotis from lower elevations, transitional areas, semiarid habitats (where dominant vegetation may include juniper, sage, and chaparral), deciduous trees along watercourses, and even agricultural areas. Although *M. evotis* is rather broadly distributed geographically, in terms of relative abundance it evidently never is particularly common.

*Myotis evotis* apparently is a "temporally opportunistic" insectivore (Fenton and Morris, 1976). Recent research on response of tympanate moths to echolocation calls of *M. evotis* suggests that these moths, and possibly other nocturnal insects, are "unable to detect typical echolocation calls of gleaning bats and thus are particularly susceptible to predation" (Faure *et al.*, 1990:843). Examination of stomach contents indicates that food items include insects of at least seven different orders. Two orders in particular seem to be especially important, Lepidoptera (moths) and Coleoptera (beetles) (Whitaker *et al.*, 1977). Intra- and interspecific niche partitioning or behavioral character displacement has been reported for this species. When a close congener, *M. auriculus*, is found sympatrically with *M. evotis*, it eats more moths than does the latter, which eats more beetles (Black, 1974; Findley, 1987). Where the two species are allopatric, male *evotis* eat significantly more lepidopterans than do females, which eat more beetles (Husar, 1976).

The long-eared myotis, a relatively late forager, is a "substrate gleaner" or "hovering gleaner" in that it feeds on or near the foliage of trees and shrubs, trunks of trees, or even on the ground. The species has demonstrated a preference for activity at relatively cool temperatures; for example, the peak netting period in southwestern New Mexico and adjacent Arizona was found to be about two hours after sunset, when the ambient temperature was about 12° C (Jones, 1965). Berna (1990) reported that long-eared myotis taken on the Kaibab Plateau in Arizona less than an hour and one-half after emergence already had stomachs filled with insects.

## Methods and Materials

Only those specimens judged to be adults, based on the following criteria, were treated in statistical analyses: specimen in adult pelage, that is, dorsal fur long and richly colored, not short, woolly, and grayish in color (as seen in juveniles); epiphyses of phalanges fused with diaphyses, giving the joint a knoblike (rather than ovoid) appearance; skull well ossified, not thinly boned, particularly as judged by the condition of the posterior portion of the cranium; sutures in the basicranial region fused.

All linear measurements given in text are in millimeters, and all weights are expressed in grams. Cranial measurements and length of forearm were taken by me and recorded to the nearest 0.01 mm using the same pair of Fowler digital calipers. Those standard external measurements judged to have been accurately recorded by the preparer were recorded directly from specimen labels. A description of external and cranial measurements used in this study (abbreviation used in text precedes the character, capital letters in parentheses refer to those used in Fig. 1) follows:

TL, total length—distance from anteriormost tip of nose to tip of posteriormost tail vertebrae.

TV, length of tail vertebrae—distance from base of tail to tip of posteriormost tail vertebrae.

HF, length of hind foot—distance from the heel to the tip of the longest toe (including claw).

EAR, length of ear—the distance from notch of ear at base to outer margin of pinna.

FA, length of forearm—distance from outermost edge of wrist (including metacarpals) to outermost edge of elbow when the wing is folded.

GLS, greatest length of skull (A-A)—greatest distance from anteriormost part of rostrum (including incisors) to posteriormost edge of supraoccipital; parallel to the long axis of the skull.

CBL, condylobasal length (B-B)—greatest distance from anteriormost edge of premaxilla to posteriormost part of occipital condyle, parallel to the long axis of the skull.

POC, postorbital constriction (C-C)—least distance across skull measured perpendicular to the long axis of the skull in region of orbit, posterior to rostrum and anterior to braincase.

ZB, zygomatic breadth (D-D)—greatest distance between outer margins of zygomatic arches perpendicular to the long axis of the skull.

MB, mastoid breadth (E-E)—greatest distance across posterior part of skull measured at region of mastoid process perpendicular to the long axis of the skull.

BBC, breadth of braincase (F-F)—greatest distance across skull, measured above zygomatic arches in temporal region perpendicular to the long axis of the skull.

RL, length of rostrum (G-G)—greatest distance, taken on the right side of the skull at a slightly oblique angle to the long axis, from anteriormost edge of premaxilla to posterior edge of zygomatic plate in the region of the orbit.

DBC, depth of braincase (H-H)—greatest distance from top of the cranium to basicranium between tympanic bullae perpendicular to the long axis of the skull.

CC, width across upper canines (I-I)—greatest distance from outermost lateral (labial) surface of one upper canine to outermost lateral surface of opposite upper canine.

M3M3, width across upper molars (J-J)—greatest distance across upper molars from outermost lateral (labial) surface, near juncture of second and third molar, to the corresponding lateral surface in the opposite quadrat.

MTR, length of maxillary toothrow (K-K)—greatest distance from posteriormost surface of third molar to anteriormost edge of canine in the same quadrat (measured on left side of skull unless teeth missing or otherwise damaged).

CM3, length of mandibular toothrow (L-L)—greatest distance from posteriormost edge of third lower molar to anteriormost edge of canine in the same quadrat (measured on the left side of skull unless teeth missing or otherwise damaged).

Color reflectance readings for red (R), green (G), and blue (B), measured as a percentage of pure white, were taken from pelage in the middorsal region of adult bats using a Photovolt Photoelectric Reflection Meter, Model 610. These readings are a measure of overall coloration in that the higher the reading, the paler the pelage color.

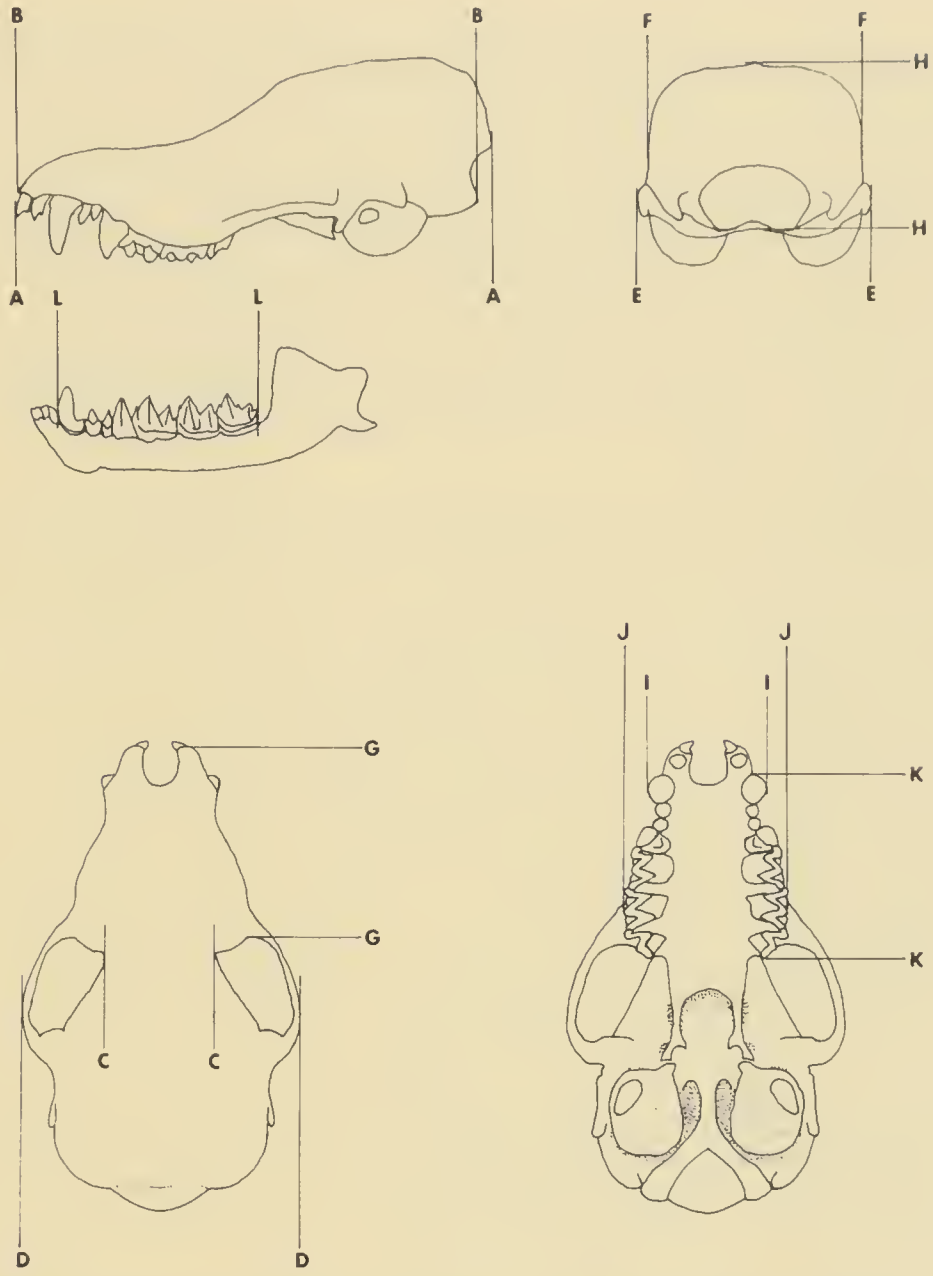



FIG. 1.—Lateral (cranium and dentary), posterior, dorsal and ventral aspect of skull of adult female *M. evotis* (TTU 38734) from Socorro County, New Mexico. Letters correspond to measurements in text.

Statistical analyses were conducted on computers (VAX 860) through Academic Computing Services at Texas Tech University and using statistical packages and procedures available through SPSS$^X$ (SPSS Inc., 1988*a*, 1988*b*). Multivariate methods (Neff and Marcus, 1980) were employed prior to most univariate analyses for reasons set forth by Willig *et al.* (1986) and Willig and Owen (1987). Several different statistical tests used in analyzing data are explained in more detail in the specific sections dealing with geographic and nongeographic variation.

Accounts of subspecies, which are arranged alphabetically, are introduced by an abbreviated synonymy that includes citations to 1) the original description and 2) first use of the current name combination if different from that originally proposed. Each account also includes a brief description of the type material and type locality, known geographic distribution of the subspecies, morphological comparisons with other races, a section for remarks in some cases, and a list of

specimens examined. Selected additional records from the literature are included, as appropriate.

On maps, specimens examined are indicated by solid symbols, whereas open symbols indicate records from the literature. Localities of record are listed alphabetically by state and therein by county. Specimens from within the same county are listed from north to south and at the same latitude from west to east. Not all localities from which specimens were examined are mapped, because undue crowding of symbols would have resulted (those not mapped are italicized in the list of specimens examined).

I am grateful to persons at several institutions for the loan of specimens or for allowing me access to specimen in their care. Acronyms used in the specimens examined section preceeds institutional name (Yates *et al.*, 1987). These are as follows: HSU—Vertebrate Museum, Humboldt State University, T. E. Lawlor and W. T. Stanley; KSC—Department of Biology, Kearney State College, J. T. Springer; KU—Museum of Natural History, University of Kansas, R. M. Timm; MHP—Museum of the High Plains, Fort Hays State University, J. R. Choate; MNA—Museum of Northern Arizona, T. J. Merkel; MSB—Museum of Southwestern Biology, University of New Mexico, J. S. Findley and T. L. Yates; MVZ—Museum of Vertebrate Zoology, University of California-Berkeley, J. L. Patton and B. Stein; MWSU—Collection of Recent Mammals, Midwestern State University, W. W. Dalquest and F. B. Stangl, Jr.; OSUFW—Department of Fisheries and Wildlife, Oregon State University, B. J. Verts and L. N. Carraway; PSM—Museum of Natural History, University of Puget Sound, E. Kritzman; UCM—Zoological Collections, University of Colorado Museum, D. M. Armstrong and S. Wu (specimens received from J. Freeman, Universidad Interamericana de Puerto Rico); UIMNH—Museum of Natural History, University of Illinois, the late M. R. Lee; UMZ—Zoology Museum, University of Montana, T. J. Pratt; USNM—United States National Museum of Natural History, D. E. Wilson and R. Fisher; UTEP—Laboratory of Environmental Ecology, University of Texas at El Paso, A. H. Harris; UW-WSM—Burke Memorial Washington State Museum, University of Washington, M. L. Johnson and J. Rozdilsky.

## Nongeographic Variation

In this study, I was not especially concerned with morphological variation due to age, because once a bat attains adult size, usually by late summer of the first year (as evinced by fusion of epiphyseal plates of phalanges, closure of sutures on the skull, and complete eruption of the permanent dention), it is sometimes difficult to distinguish young adults from other adults, and there appear to be no differences in either external or cranial size. Therefore, all bats showing the characteristics mentioned above were treated as adults, and no attempt was made to subdivide them into discrete age classes.

TABLE 1.—*Results of univariate (ONEWAY ) tests, with sex as the main effect, for a sample of* Myotis evotis *from Socorro County, New Mexico. Characters and significance levels* (P) *are given.*

| Character | *P* |
|---|---|
| Length of forearm | 0.0002 |
| Greatest length of skull | 0.0171 |
| Condylobasal length | 0.0183 |
| Postorbital constriction | 0.2993 |
| Zygomatic breadth | 0.7787 |
| Mastoid breadth | 0.0282 |
| Breadth of braincase | 0.7534 |
| Length of rostrum | 0.1275 |
| Depth of braincase | 0.2509 |
| Width across upper canines | 0.5636 |
| Width across upper molars | 0.1289 |
| Length of maxillary toothrow | 0.0031 |
| Length of mandibular toothrow | 0.0378 |
| Percent reflectance of red | 0.9798 |
| Percent reflectance of green | 0.9176 |
| Percent reflectance of blue | 0.4472 |

In order to document nongeographic variation in *Myotis evotis*, the sample with the largest number of individuals ($N$ =146) from one geographic location (Socorro County, New Mexico) was chosen for statistical testing. A one-way multivariate analysis of variance (MANOVA) was performed (SPSS, Inc., 1988*b*), with sex as the main factor, on 16 characters. No significant difference ($P = 0.280$) was detected between males and females in this sample for these characters.

Following this multivariate procedure, univariate analysis of variance tests (ONEWAY) was performed (SPSS, Inc., 1988*b*) to analyze each character. Results of these univariate tests are presented in Table 1. Descriptive statistics (males and female treated separately), for 16 characters (FA, GLS, CBL, ZB, POC, MB, BBC, RL, DBC, CC, M3M3, MTR, CM3, R, G, and B) are presented in Table 2.

Univariate tests detected significant differences ($P < 0.05$) between males and females (females the larger) for length of forearm, greatest length of skull, condylobasal length, mastoid breadth, length of maxillary toothrow, and length of mandibular toothrow. No significant difference was detected in color reflectance readings between sexes in this sample, although females average slightly darker than males in all three color reflectance readings.

Except for postorbital constriction, females average slightly larger than males in all mensural characters studied. As previously mentioned, it has been documented that males of *M. evotis* selectively feed on moths (soft-bodied insects), whereas females feed on beetles (hard-bodied insects). Larger size of cranium in females

TABLE 2.—*Descriptive statistics for 16 characters from a sample of* Myotis evotis *(males and females reported separately) from Socorro County, New Mexico. Abbreviations used are: SD (standard deviation), N (sample size), and CI (95 percent confidence interval).*

| Sex | Mean | SD | N | CI |
|---|---|---|---|---|
| | | Length of forearm | | |
| M | 39.4 | 0.892 | 63 | 39.18–39.63 |
| F | 40.1 | 1.146 | 75 | 39.82–40.34 |
| | | Greatest length of skull | | |
| M | 16.55 | 0.294 | 46 | 16.46–16.63 |
| F | 16.69 | 0.304 | 65 | 16.61–16.76 |
| | | Condylobasal length | | |
| M | 15.53 | 0.343 | 45 | 15.42–15.62 |
| F | 15.68 | 0.307 | 63 | 15.59–15.75 |
| | | Zygomatic breadth | | |
| M | 9.88 | 0.259 | 39 | 9.79–9.96 |
| F | 9.90 | 0.277 | 55 | 9.82–9.97 |
| | | Postorbital constriction | | |
| M | 3.87 | 0.111 | 49 | 3.83–3.90 |
| F | 3.85 | 0.122 | 67 | 3.81–3.87 |
| | | Mastoid breadth | | |
| M | 7.99 | 0.156 | 48 | 7.94–8.03 |
| F | 8.05 | 0.147 | 66 | 8.01–8.08 |
| | | Breadth of braincase | | |
| M | 7.33 | 0.170 | 49 | 7.27–7.37 |
| F | 7.34 | 0.160 | 67 | 7.29–7.37 |
| | | Length of rostrum | | |
| M | 7.32 | 0.180 | 48 | 7.26–7.36 |
| F | 7.38 | 0.228 | 67 | 7.32–7.43 |
| | | Depth of braincase | | |
| M | 5.19 | 0.181 | 47 | 5.13–5.24 |
| F | 5.23 | 0.171 | 65 | 5.18–5.26 |
| | | Width across upper molars | | |
| M | 6.22 | 0.184 | 48 | 6.17–6.27 |
| F | 6.28 | 0.178 | 67 | 6.23–6.31 |
| | | Length of maxillary toothrow | | |
| M | 6.37 | 0.125 | 49 | 6.33–6.40 |
| F | 6.45 | 0.159 | 67 | 6.40–6.48 |

TABLE 2.—*Continued.*

| Sex | Mean | SD | N | CI |
|---|---|---|---|---|
| | | Length of mandibular toothrow | | |
| M | 6.88 | 0.171 | 48 | 6.82–6.92 |
| F | 6.95 | 0.204 | 67 | 6.90–7.00 |
| | | Percent reflectance of red | | |
| M | 15.8 | 1.871 | 16 | 14.79–16.78 |
| F | 15.7 | 2.251 | 19 | 14.68–16.85 |
| | | Percent reflectance of green | | |
| M | 7.9 | 1.031 | 16 | 7.39–8.49 |
| F | 7.9 | 1.339 | 19 | 7.25–8.54 |
| | | Percent reflectance of blue | | |
| M | 6.2 | 0.947 | 16 | 5.68–6.69 |
| F | 6.5 | 1.207 | 19 | 5.89–7.06 |

(for example, GLS, CBL, MB) to accommodate masticatory musculature, and longer toothrows (MTR, CM3) could represent character displacement coincidental with behavioral displacement or niche partitioning (Husar, 1976) known to occur in this species. Another possible scenario to explain larger size in females is the "big mother" hypothesis advanced by Ralls (1976). According to this scheme, larger mothers produce larger offspring, which mature faster and thus have a better chance of achieving adult size and fending for themselves more quickly than do smaller young produced by smaller mothers.

## GEOGRAPHIC VARIATION

Specimens of *M. evotis* were grouped into geographic samples that then could be tested using appropriate statistical methods. Care was taken when combining individuals into groups so as not to cross currently recognized subspecific boundaries as mapped by Hall (1981), or to group specimens from different physiographic regions or from areas that crossed potential major biogeographic barriers. Political boundaries, however, were ignored when forming sample groups.

Grouped samples used in this study are from the geographic areas shown in Figure 2. Six were judged to contain a large enough number of specimens to be used in preliminary analyses, whereas the others (smaller sample sizes or single individuals) were treated in subsequent tests or assessed individually based on examination of specimens.

My six groups are from distinct geographic regions and are numbered and referenced in text, according to region as follows: 1, Pacific Northwest (PACNW); 2, Southern California (SOCAL); 3a, Northern Rocky Mountains-East (NROCE); 3b,

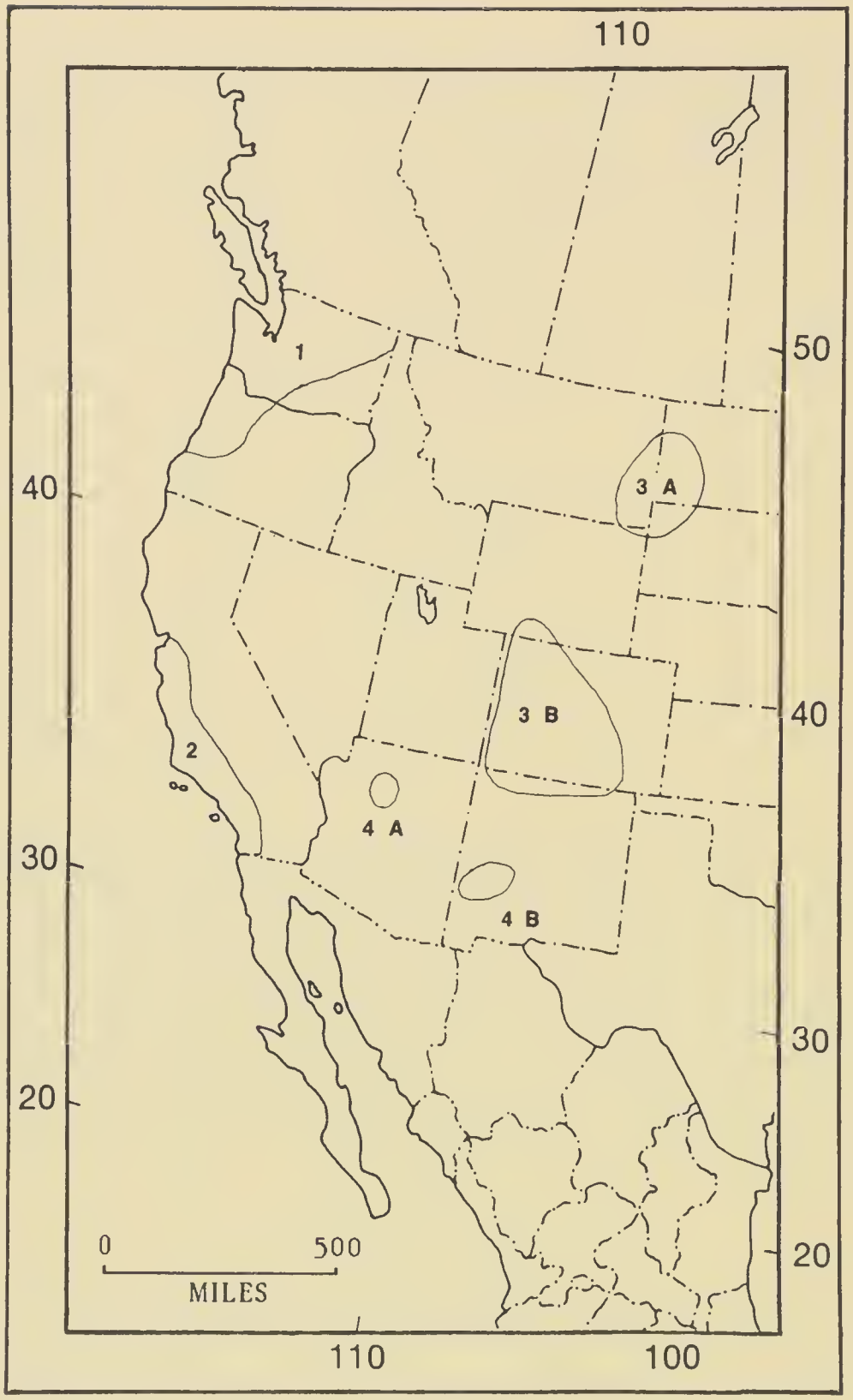



FIG. 2.—Map showing geographic locality of samples (groups 1, 2, 3a, 3b, 4a, and 4b) of *Myotis evotis* used in preliminary statistical tests.

Northern Rocky Mountains-West (NROCW); 4a, Southwestern United States-West (SWUSW); 4b, Southwestern United States-East (SWUSE). Specific localities that define these groups are listed below. The a and b designations are used within 3 and 4 because these samples are combined for analysis later in this chapter.

Group 1 (PACNW)—Clark, Douglas, Gray Harbor, Kittitas, and Pierce counties, Washington; Benton, Clackamas, Clatsop, Coos, Lane, Lincoln, and Tillamook counties, Oregon.

Group 2 (SOCAL)—Alemeda, Monterey, Los Angeles, San Diego, San Luis Obispo, Santa Barbara, Santa Clara, and Santa Cruz counties, California.

Group 3a (NROCE)—Carter and Powder River counties, Montana; Billings and Dunn counties, North Dakota; Harding County, South Dakota.

Group 3b (NROCW)—Alamosa, Archuleta, Delta, Garfield, Gunnison, Las Animas, Mesa, Moffat, Montezuma, Rio Blanco, Routt, and Saguache counties, Colorado; Colfax, Rio Arriba, Taos, and Union counties, New Mexico; Carbon and Uinta counties, Wyoming.

Group 4a (SWUSW)—Coconino County, Arizona.

Group 4b (SWUSE)—Catron and Socorro counties, New Mexico.

Multivariate statistical procedures have been used to analyze geographic variation in several mammalian taxa including kangaroo rats (Genoways and Jones, 1971), *Myotis* (Findley, 1972; Bogan, 1975), pallid bats (Manning *et al.*, 1988), rice rats (Humphrey and Setzer, 1989), and pocket gophers (Hollander, 1990), to name but a few. Initially, the six groups of *M. evotis* (those judged to have adequate sample sizes) were tested using a two-way multivariate analysis of variance (MANOVA) procedure (SPSS, Inc., 1988*b*) with geographic locality and sex as main effects. The absence of significant interaction ($P = 0.068$) between main effects indicates that secondary sexual differences ($P = 0.008$) are consistant irrespective of locality; in other words, the observed geographic variation is consistantly displayed. Unfortunately, this test does not reveal the pattern of geographic variation.

One-way analysis of variance (ANOVA) was used to test the hypothesis that group means of dependent variables are equal. Each dependent variable (FA, GLS, CBL, POC, MB, BBC, RL, DBC, CC, M3M3, MTR, CM3, R, G, B) was analyzed using the procedure ONEWAY, with geographic locality as the main effect. Highly significant differences ($P < 0.001$) were detected between group means for each character in both sexes. Multiple range tests, Scheffe's and Student-Newman-Kuels, both of which are conservative, were used to indicate nonsignificant subsets of group means. Results of Scheffe's test are reported here, not only because that test is conservative, but also because Scheffe's test is mathematically equivalent to sum of squares simultaneous test procedure (SS-STP). This procedure (SS-STP) is a method by which all possible sets of comparisons among means can be tested while controlling the experiment-wise error rate (Sokal and Rohlf, 1981).

As an overall measure of similarity or "nearness," cluster analysis (using procedure CLUSTER—SPSS-X, 1988*b*), was performed using means of 15 dependent variables for the six geographic samples. UPGMA (unweighted pair group method using arithmetic average), measuring Euclidean (unweighted) distance algorithm, was used in this analysis. Resulting dendrograms from these analyses are presented in Fig. 3.

Principal components analysis (PCA), using procedure FACTOR (SPSS-X, 1988*a*), was used to identify those factors that account for or explain the largest percentage of variation in the sample. Results of these analyses are given in Table 3.

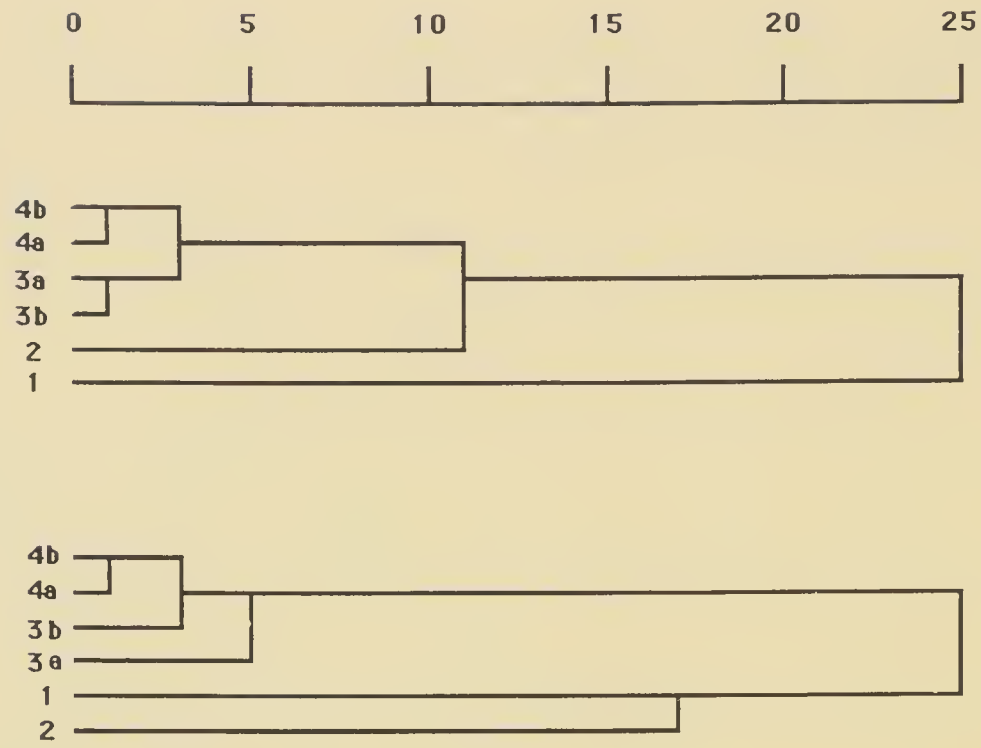



FIG. 3.—Dendrograms produced by cluster analysis (UPGMA, Euclidean distance) of mean values of dependent variables for males (above) and females (below), in six initial sample groups (see text). Horizontal bar indicates rescaled morphometric differences between groups.

Note that the first three factors explain 76.9 and 80.3 percent of the total variation in males and females, respectively. Factor matrices from correlations among 15 characters used in PCA are given in Table 4 (males) and Table 5 (females).

Two-dimensional plots of the first three principal components are given in Fig. 4. Factor loadings on the first axis all were positive, with highest values for greatest length of skull and condylobasal length. This suggests that the first axis may be interpreted as a general size axis. Members of groups 4a and 4b (far right on axis one) had larger skulls than those in groups 1 and 2 (far left of this axis). Factor loadings on the second axis had highest positive values for color reflectance readings, thereby suggesting that factor two is a general axis for pelage color. Individuals in group 1 had the darkest pelage, whereas those in group 3a averaged palest. Axis three may be interpreted as another general size axis, in this instance for cranial width, because breadth of braincase (males) and postorbital constriction (females) had highest loading values.

Using results of my previous analyses (MANOVA, ONEWAY, CLUSTER, and FACTOR), and because the geographic samples involved have no potential biogeographic barriers between them, some of the original six sample groups were pooled. Group 3a and group 3b were combined (NROCK) because these samples differed in only one character in males (percent reflectance of blue), and only two characters in females (POC and M3M3). Likewise, group 4a and group 4b were joined (SWUSA) because they differed only in one character, M3M3 (and only in males).

TABLE 3.—*Results of principal components analysis (FACTOR) of 15 characters for each sex. Unique variance attributed to each factor and the cumulative percentage of variance attributable to that factor (and those that precede it in the table) are given.*

| | Males | | Females | |
|---|---|---|---|---|
| Factor | Unique variance | Cumulative percent | Unique variance | Cumulative percent |
| 1 | 53.0 | 53.0 | 58.2 | 58.2 |
| 2 | 15.2 | 68.2 | 15.2 | 73.4 |
| 3 | 8.7 | 76.9 | 6.9 | 80.3 |
| 4 | 5.0 | 81.8 | 4.6 | 84.9 |
| 5 | 4.1 | 85.9 | 3.5 | 88.4 |
| 6 | 3.8 | 89.7 | 2.9 | 91.3 |
| 7 | 2.1 | 91.8 | 2.2 | 93.5 |
| 8 | 1.9 | 93.7 | 1.5 | 95.0 |
| 9 | 1.5 | 95.1 | 1.2 | 96.2 |
| 10 | 1.3 | 96.4 | 1.1 | 97.3 |
| 11 | 1.0 | 97.4 | 1.0 | 98.3 |
| 12 | 0.8 | 98.3 | 0.7 | 99.0 |
| 13 | 0.8 | 99.0 | 0.5 | 99.5 |
| 14 | 0.7 | 99.7 | 0.3 | 99.8 |
| 15 | 0.3 | 100.0 | 0.2 | 100.0 |

TABLE 4.—*Sorted factor matrix for males of correlations among 15 characters studied. High loadings indicate strong correlation with vector. Breaks in columns indicate associations between characters and factor levels.*

| | Factor I | Factor II | Factor III |
|---|---|---|---|
| GLS | .93714 | −.08205 | −.15147 |
| CBL | .91748 | −.13228 | −.18502 |
| RL | .88953 | −.04739 | −.27261 |
| CM3 | .88325 | −.10541 | −.27275 |
| MTR | .85108 | −.10154 | −.32247 |
| FA | .84949 | −.14659 | −.07882 |
| CC | .83136 | −.12205 | .06165 |
| M3M3 | .82155 | −.05670 | .00217 |
| MB | .78404 | −.17736 | .35481 |
| DBC | .55720 | .00749 | .37610 |
| POC | .47540 | −.18202 | .45471 |
| G | .34891 | .88664 | .07918 |
| B | .38345 | .81671 | .14783 |
| R | .46211 | .79925 | −.06064 |
| BBC | .46843 | −.16638 | .69011 |

TABLE 5.—*Sorted factor matrix for females of correlations among 15 characters studied. High loadings indicate strong correlation with vector. Breaks in columns indicate associations between characters and factor levels.*

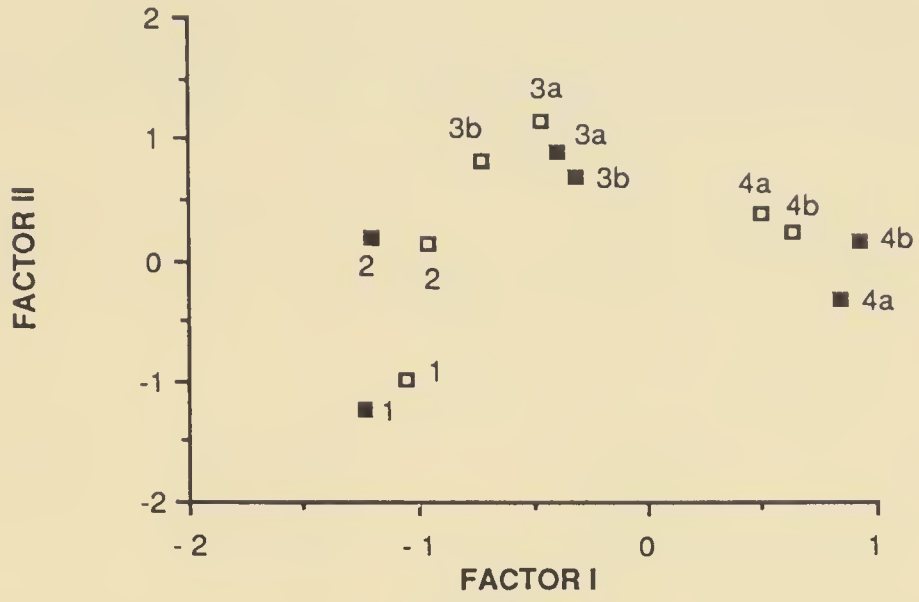
| | Factor I | Factor II | Factor III |
|---|---|---|---|
| GLS | .95711 | −.02996 | −.13848 |
| CBL | .95165 | −.04060 | −.19276 |
| MTR | .90765 | −.06454 | −.27660 |
| CM3 | .89727 | −.01569 | −.21413 |
| RL | .88890 | −.03817 | −.21939 |
| FA | .85895 | −.08144 | −.13495 |
| M3M3 | .85277 | −.14274 | .05800 |
| MB | .83607 | −.17039 | .10056 |
| CC | .81971 | −.27345 | −.03545 |
| BBC | .53851 | −.31783 | .35958 |
| DBC | .53851 | −.29292 | .45010 |
| G | .54874 | .78177 | .20067 |
| B | .51503 | .75715 | .28981 |
| R | .56354 | .73334 | .13234 |
| POC | .29783 | −.48007 | .55006 |

Results of pooling was formation of four samples (3a and 3b, hereafter group 3, and 4a and 4b, hereafter group 4 ): group 1 (PACNW); group 2 (SOCAL); group 3 (NROCK); and group 4 (SWUSA).

These four newly-constituted groups were tested using a two-way multivariate analysis of variance (MANOVA) procedure (SPSS, Inc., 1988*b*), with geographic locality and sex as main effects. Results of this test indicated that there is a significant difference ($P < 0.001$) between means of at least two localities, and between sexes ($P < 0.010$); again, however, there was no indication of interaction between geographic locality and sex ($P = 0.113$).

Each dependent variable (FA, GLS, CBL, POC, MB, BBC, RL, DBC, CC, M3M3, MTR, CM3, R, G, B) was analyzed separately using the procedure ONEWAY with geographic locality (groups 1–4) as main effect. Significant differences were detected between group means for both sexes. Multiple range tests (results of Scheffe's test) were used to indicate nonsignificant subsets of these group means (Table 6).

These results indicate that each of the four groups is statistically distinct from the others. Therefore, these four samples (groups 1–4 as redefined above) were analyzed using discriminant function analysis (DFA). Individuals were classified



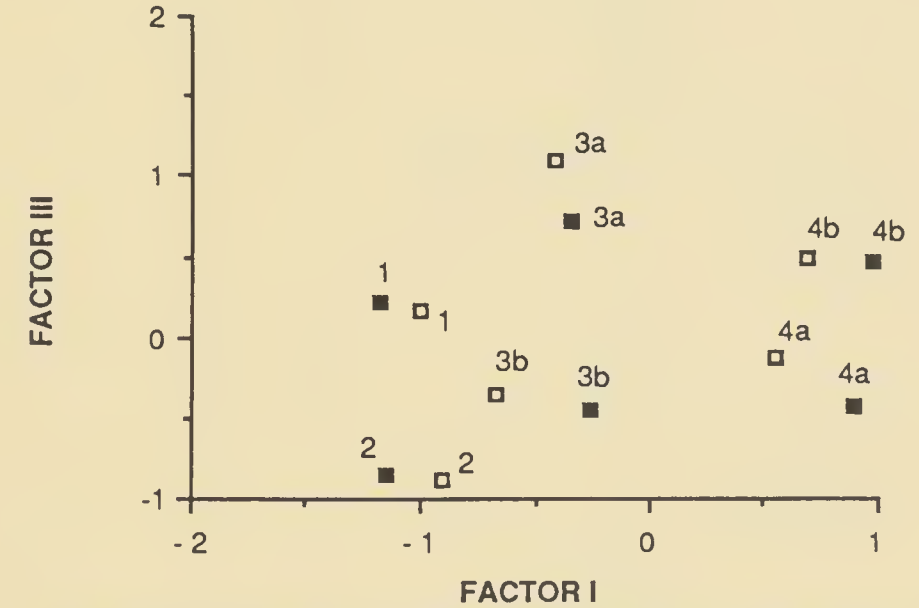




FIG. 4.—Two-dimensional plots of the first three principal components, in six initial sample groups (see text). Factor I against Factor II (above) Factor I against Factor III (below); males (solid), females (open symbols).

into one of four mutually exclusive groups on the basis of a set of morphological characters using procedure (DISCRIMINANT) as defined in SPSS-X Inc. (1988*a*). Results of this test indicate that significant differences (F-ratio < 0.001) exist between all possible pairs of these four groups. Classification results of this test are presented in Table 7 (males) and Table 8 (females).

It was decided *a priori* not to recognize any sample as a taxonomic entity unless the members of that unit could be correctly classified at least 75 percent of the time (frequently referred to as the 75 percent rule). This rationale is discussed in some detail by Thorpe (1987).

TABLE 6.—*Results of one-way ANOVAs (ONEWAY ) for 15 characters used in analyses. Results of Scheffe's multiple range test (MRT ), for each sex separately, are presented. An asterisk (*) in the column following group number denotes pairs of groups significantly different at the 0.05 level. Other abbreviations used are: CI (95 percent confidence interval ), N (sample size), and* P (*significance level* ).

| Group | MRT | Mean (N) | CI | *P* |
|---|---|---|---|---|
| | | Length of forearm | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 35.3 (19) | 34.68 – 35.99 | 0.000 |
| 1 | | 36.3 (21) | 35.68 – 36.86 | |
| 3 | * * | 38.2 (53) | 37.97 – 38.52 | |
| 4 | * * * | 39.2 (95) | 39.03 – 39.42 | |
| Females | | | | |
| | 2 1 3 | | | |
| 2 | | 35.8 (16) | 35.24 – 36.33 | 0.000 |
| 1 | * | 36.8 (29) | 36.32 – 37.19 | |
| 3 | * * | 38.6 (38) | 38.26 – 38.90 | |
| 4 | * * * | 40.0 (85) | 39.74 – 40.22 | |
| | | Greatest length of skull | | |
| Males | | | | |
| | 1 2 3 | | | |
| 1 | | 15.46 (21) | 15.32 – 15.61 | 0.000 |
| 2 | | 15.45 (18) | 15.26 –15.72 | |
| 3 | * * | 16.00 (45) | 15.91 – 16.08 | |
| 4 | * * * | 16.51 (76) | 16.45 – 16.58 | |
| Females | | | | |
| | 1 2 3 | | | |
| 1 | | 15.38 (28) | 15.18 – 15.59 | 0.000 |
| 2 | | 15.60 (16) | 15.43 – 15.76 | |
| 3 | * * | 16.01 (34) | 15.89 – 16.14 | |
| 4 | * * * | 16.66 (75) | 16.59 – 16.73 | |
| | | Condylobasal length | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 14.48 (18) | 14.29 – 14.68 | 0.000 |
| 1 | | 14.48 (20) | 14.32 – 14.65 | |
| 3 | * * | 15.00 (45) | 14.92 – 15.07 | |
| 4 | * * * | 15.50 (76) | 15.43 – 15.58 | |
| Females | | | | |
| | 1 2 3 | | | |
| 1 | | 14.43 (28) | 14.25 – 14.62 | 0.000 |
| 2 | | 14.56 (16) | 14.37 – 14.74 | |
| 3 | * * | 14.99 (35) | 14.86 – 15.11 | |
| 4 | * * * | 15.66 (73) | 15.59 – 15.73 | |

TABLE 6.—*Continued.*

| Group | MRT | Mean (N) | CI | *P* |
|---|---|---|---|---|
| | | Postorbital constriction | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 3.68 (18) | 3.61 – 3.75 | 0.000 |
| 1 | * | 3.81 (22) | 3.77 – 3.86 | |
| 3 | * | 3.82 (47) | 3.79 – 3.86 | |
| 4 | * | 3.85 (80) | 3.82 – 3.88 | |
| Females | | | | |
| | 2 3 1 | | | |
| 2 | | 3.69 (16) | 3.62 – 3.76 | 0.000 |
| 3 | | 3.76 (38) | 3.72 – 3.80 | |
| 1 | * | 3.83 (28) | 3.80 – 3.87 | |
| 4 | * * | 3.84 (77) | 3.81 – 3.87 | |
| | | Mastoid breadth | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 7.66 (18) | 7.58 – 7.74 | 0.000 |
| 1 | | 7.74 (21) | 7.69 – 7.79 | |
| 3 | * | 7.83 (42) | 7.77 – 7.88 | |
| 4 | * * * | 7.96 (79) | 7.92 – 8.00 | |
| Females | | | | |
| | 2 1 3 | | | |
| 2 | | 7.70 (16) | 7.62 – 7.78 | 0.000 |
| 1 | | 7.72 (27) | 7.64 – 7.80 | |
| 3 | * * | 7.87 (34) | 7.80 – 7.93 | |
| 4 | * * * | 8.03 (76) | 8.00 – 8.07 | |
| | | Breadth of braincase | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 7.19 (18) | 7.09 – 7.29 | .0344 |
| 1 | | 7.20 (21) | 7.15 – 7.27 | |
| 3 | | 7.21 (43) | 7.20 – 7.29 | |
| 4 | | 7.23 (80) | 7.26 – 7.34 | |
| Females | | | | |
| | 2 1 3 | | | |
| 2 | | 7.09 (16) | 7.02 – 7.17 | 0.001 |
| 1 | | 7.18 (28) | 7.10 – 7.25 | |
| 3 | | 7.21 (36) | 7.16 – 7.26 | |
| 4 | * * * | 7.32 (77) | 7.29 – 7.36 | |

TABLE 6.—*Continued.*

| Group | MRT | Mean (N) | CI | *P* |
|---|---|---|---|---|
| | | Length of rostrum | | |
| Males | | | | |
| | 1 2 3 | | | |
| 1 | | 6.73 (22) | 6.64 – 6.83 | 0.000 |
| 2 | | 6.75 (18) | 6.63 – 6.87 | |
| 3 | * * | 7.04 (48) | 6.99 – 7.08 | |
| 4 | * * * | 7.31 (79) | 7.27 – 7.35 | |
| Females | | | | |
| | 1 2 3 | | | |
| 1 | | 6.77 (28) | 6.67 – 6.87 | 0.000 |
| 2 | | 6.80 (16) | 6.68 – 6.92 | |
| 3 | * * | 7.02 (37) | 6.95 – 7.08 | |
| 4 | * * * | 7.38 (77) | 7.33 – 7.43 | |
| | | Depth of braincase | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 4.94 (17) | 4.86 – 5.03 | 0.000 |
| 1 | | 5.07 (20) | 5.01 – 5.12 | |
| 3 | * | 5.13 (44) | 5.09 – 5.18 | |
| 4 | * * | 5.18 (78) | 5.14 – 5.22 | |
| Females | | | | |
| | 2 1 3 | | | |
| 2 | | 4.95 (16) | 4.87 – 5.03 | 0.000 |
| 1 | | 5.07 (28) | 5.01 – 5.14 | |
| 3 | * | 5.15 (32) | 5.09 – 5.22 | |
| 4 | * * | 5.22 (75) | 5.18 – 5.26 | |
| | | Width across upper canines | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 3.54 (18) | 3.45 – 3.62 | 0.000 |
| 1 | * | 3.67 (22) | 3.61 – 3.72 | |
| 3 | * * | 3.79 (48) | 3.75 – 3.82 | |
| 4 | * * * | 3.92 (78) | 3.89 – 3.95 | |
| Females | | | | |
| | 2 1 3 | | | |
| 2 | | 3.54 (16) | 3.48 – 3.60 | 0.000 |
| 1 | * | 3.70 (28) | 3.64 – 3.77 | |
| 3 | * | 3.76 (36) | 3.72 – 3.80 | |
| 4 | * * * | 3.97 (77) | 3.94 – 4.00 | |

Table 6.—*Continued.*

| Group | MRT | Mean (N) | CI | *P* |
|---|---|---|---|---|
| | | Width across upper molars | | |
| Males | | | | |
| | 2 1 3 | | | |
| 2 | | 5.70 (18) | 5.59 – 5.82 | .0000 |
| 1 | | 5.75 (22) | 5.67 – 5.84 | |
| 3 | * * | 6.02 (48) | 5.96 – 6.08 | |
| 4 | * * * | 6.16 (79) | 6.12 – 6.20 | |
| Females | | | | |
| | 2 1 3 | | | |
| 2 | | 5.81 (16) | 5.74 – 5.87 | .0000 |
| 1 | | 5.82 (28) | 5.74 – 5.92 | |
| 3 | * * | 6.00 (38) | 5.94 – 6.07 | |
| 4 | * * * | 6.26 (77) | 6.22 – 6.30 | |
| | | Length of maxillary toothrow | | |
| Males | | | | |
| | 1 2 3 | | | |
| 1 | | 5.85 (22) | 5.79 – 5.92 | 0.000 |
| 2 | | 5.90 (18) | 5.74 – 6.07 | |
| 3 | * * | 6.08 (47) | 6.04 – 6.11 | |
| 4 | * * * | 6.35 (80) | 6.32 – 6.38 | |
| Females | | | | |
| | 1 2 3 | | | |
| 1 | | 5.83 (28) | 5.72 – 5.93 | 0.000 |
| 2 | | 5.88 (16) | 5.77 – 6.00 | |
| 3 | * * | 6.07 (38) | 6.01 – 6.12 | |
| 4 | * * * | 6.44 (77) | 6.40 – 6.47 | |
| | | Length of mandibular toothrow | | |
| Males | | | | |
| | 1 2 3 | | | |
| 1 | | 6.28 (22) | 6.20 – 6.36 | 0.000 |
| 2 | | 6.28 (18) | 6.19 – 6.37 | |
| 3 | * * | 6.55 (47) | 6.50 – 6.60 | |
| 4 | * * * | 6.86 (79) | 6.82 – 6.89 | |
| Females | | | | |
| | 1 2 3 | | | |
| 1 | | 6.26 (27) | 6.15 – 6.37 | 0.000 |
| 2 | | 6.34 (16) | 6.23 – 6.46 | |
| 3 | * * | 6.58 (38) | 6.52 – 6.64 | |
| 4 | * * * | 6.94 (77) | 6.89 – 7.00 | |

TABLE 6.—*Continued.*

| Group | MRT | Mean (N) | CI | *P* |
|---|---|---|---|---|
| | | Percent reflectance of red | | |
| Males | | | | |
| | 1 2 4 | | | |
| 1 | | 8.9 (15) | 7.77 – 10.09 | 0.000 |
| 2 | * | 13.8 (15) | 12.52 – 15.14 | |
| 4 | * | 14.6 (43) | 13.90 – 15.33 | |
| 3 | * | 15.9 (31) | 14.93 – 16.78 | |
| Females | | | | |
| | 1 2 4 | | | |
| 1 | | 9.6 (23) | 8.80 – 10.42 | 0.000 |
| 2 | * | 13.6 (15) | 11.67 – 15.53 | |
| 4 | * * | 15.9 (29) | 15.07 – 16.65 | |
| 3 | * * | 16.5 (26) | 15.38 – 17.58 | |
| | | Percent reflectance of green | | |
| Males | | | | |
| | 1 4 2 | | | |
| 1 | | 4.9 (15) | 4.39 – 5.41 | 0.000 |
| 4 | * | 7.1 (43) | 6.72 – 7.53 | |
| 2 | * | 7.2 (15) | 6.30 – 8.10 | |
| 3 | * | 8.3 (31) | 7.76 – 8.76 | |
| Females | | | | |
| | 1 2 4 | | | |
| 1 | | 4.8 (23) | 4.43 – 5.14 | 0.000 |
| 2 | * | 6.9 (15) | 5.93 – 7.87 | |
| 4 | * | 8.1 (29) | 7.60 – 8.54 | |
| 3 | * * | 8.6 (26) | 7.87 – 9.24 | |
| | | Percent reflectance of blue | | |
| Males | | | | |
| | 1 2 4 | | | |
| 1 | | 4.0 (15) | 3.64 – 4.36 | 0.000 |
| 2 | * | 5.8 (15) | 5.00 – 6.53 | |
| 4 | * | 5.8 (43) | 5.45 – 6.08 | |
| 3 | * * * | 7.0 (31) | 6.44 – 7.53 | |
| Females | | | | |
| | 1 2 4 | | | |
| 1 | | 3.9 (23) | 3.63 – 4.24 | 0.000 |
| 2 | * | 5.7 (15) | 4.91 – 6.42 | |
| 4 | * | 6.5 (29) | 6.04 – 6.86 | |
| 3 | * * | 6.9 (26) | 6.30 – 7.50 | |

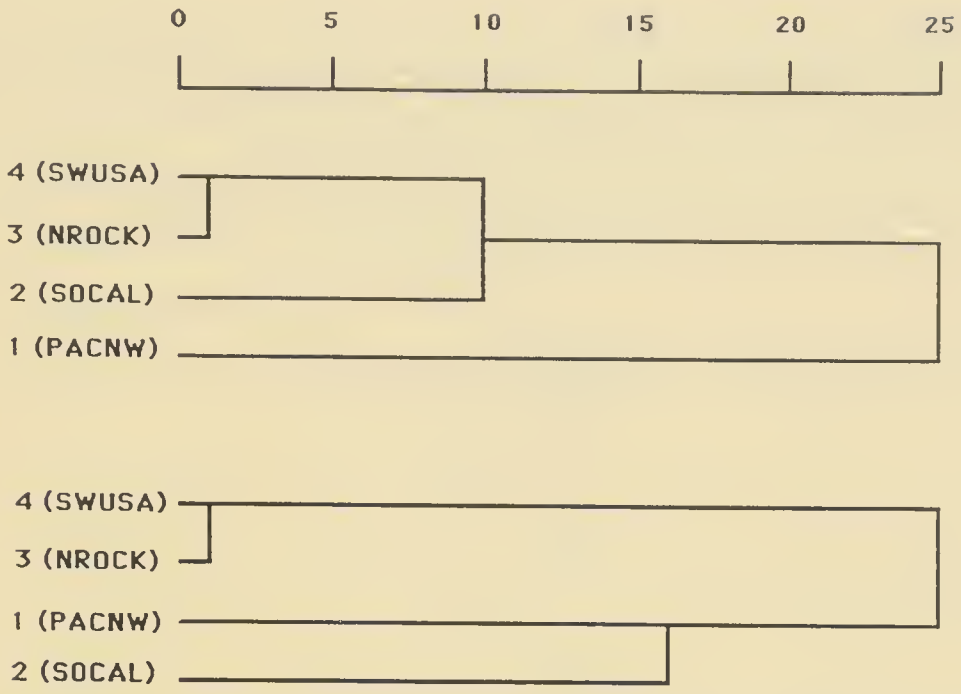



FIG. 5.—Dendrograms produced by cluster analysis (UPGMA, Euclidean distance) for males (above) females (below) from reconstituted groups 1–4 as described in text. Horizontal bar indicates rescaled morphometric differences between groups.

In previous analyses (two-way MANOVAs), there was an indication of significant difference between sexes, but no significant interaction between sex and geographic locality. *A posteriori,* I ran separate MANOVAs, with sex as the main effect, to identify in which of the six initial samples significant differences between males and females occurred. Remember that in the sample from Socorro County, New Mexico (sample used in analysis of nongeographic variation), there was no significant difference between sexes; females, however, averaged slightly larger than males. *A posteriori* tests suggest no significant difference between sexes at any locality.

Samples from SOCAL and BAJAM (Baja Cailfornia, México) were tested using a one-way multivariate analysis of variance (MANOVA) procedure (SPSS, Inc., 1988*b*) with geographic locality as the main effect. Results of this test indicated no significant difference ($P = 0.072$) between the two geographic localities. These results must be interpreted with caution, however, because the sample size for *milleri* totaled only eight individuals, two females and six males. The low power of this test, which results from small sample size, and the inability to control for variation due to sex would require large interlocality differences to produce significance. Actual differences between means from SOCAL and BAJAM were of the same magnitude as those between statistically distinct localities (see Table 6). I chose the systematically conservative approach in treating these two samples separately. Descriptive statistics for these dependent variables are presented in Table 9. All members of the samples were correctly classified using discriminant function analysis.

TABLE 7.—*Results of discriminant function classification for males, using the four groups formed by cluster analysis. Sample size (N) and predicted group membership are given in the table. Number of cases correctly assigned (percentage in parentheses) to each group is given. Percent of "grouped" cases correctly classified was 88.76 percent.*

| Actual group membership | N | Predicted group membership | | | |
|---|---|---|---|---|---|
| | | PACNW | SOCAL | NROCK | SWUSA |
| PACNW | 13 | 12 (92.3) | 1 (7.7) | 0 (0.0) | 0 (0.0) |
| SOCAL | 14 | 1 (7.1) | 12 (85.7) | 1 (7.1) | 0 (0.0) |
| NROCK | 26 | 0 (0.0) | 2 (7.7) | 23 (88.5) | 1 (3.8) |
| SWUSA | 36 | 0 (0.0) | 0 (0.0) | 4 (11.1) | 32 (88.9) |

TABLE 8.—*Results of discriminant function classification for females, using the four groups formed by cluster analysis. Sample size (N) and predicted group membership are given in the table. Number of cases correctly assigned (percentage in parentheses) to each group is given. Percent of "grouped" cases correctly classified was 92.68 percent.*

| Actual group membership | N | Predicted group membership | | | |
|---|---|---|---|---|---|
| | | PACNW | SOCAL | NROCK | SWUSA |
| PACNW | 20 | 19 (95.0) | 1 (5.0) | 0 (0.0) | 0 (0.0) |
| SOCAL | 15 | 0 (0.0) | 14 (93.3) | 1 (6.7) | 0 (0.0) |
| NROCK | 18 | 1 (5.6) | 0 (0.0) | 16 (88.9) | 1 (5.6) |
| SWUSA | 29 | 0 (0.0) | 0 (0.0) | 2 (6.9) | 27 (93.1) |

As an overall measure of similarity or "nearness," cluster analysis (using procedure CLUSTER—SPSS-X, 1988*b*), was performed using means of 15 dependent variables for groups 1–4 and the Baja California sample. UPGMA (unweighted pair group method using arithmetic average), measuring Euclidean (unweighted)

TABLE 9.—*Descriptive statistics for 15 characters from a sample of* Myotis *from Sierra San Pedro Mártir, Baja California. Abbreviations used are:* SD *(standard deviation), N (sample size), and CI (95 percent confidence interval).*

| Sex | Mean | SD | N | CI |
|---|---|---|---|---|
| | | Length of forearm | | |
| M | 34.2 | 1.062 | 6 | 33.09 – 35.32 |
| F | 35.3 | 0.226 | 2 | 33.26 – 37.32 |
| | | Greatest length of skull | | |
| M | 15.38 | 0.258 | 4 | 14.97 – 15.79 |
| F | 15.12 | 0.170 | 2 | 13.59 – 16.64 |
| | | Condylobasal length | | |
| M | 14.16 | 0.438 | 4 | 13.47 –14.86 |
| F | 14.37 | 0.191 | 2 | 12.65 – 16.08 |
| | | Postorbital constriction | | |
| M | 3.61 | 0.120 | 5 | 3.46 – 3.76 |
| F | 3.66 | 0.050 | 2 | 3.21 – 4.10 |
| | | Mastoid breadth | | |
| M | 7.41 | 0.179 | 4 | 7.12 – 7.70 |
| F | 7.64 | 0.035 | 2 | 7.32 – 7.95 |
| | | Breadth of braincase | | |
| M | 7.08 | 0.153 | 4 | 6.84 – 7.32 |
| F | 7.01 | 0.042 | 2 | 6.63 – 7.39 |
| | | Length of rostrum | | |
| M | 6.64 | 0.118 | 5 | 6.49 – 6.78 |
| F | 6.52 | 0.205 | 2 | 4.67 – 8.35 |
| | | Depth of braincase | | |
| M | 4.53 | 0.053 | 3 | 4.40 – 4.66 |
| F | 4.74 | 0.050 | 2 | 4.29 – 5.18 |
| | | Width across upper canines | | |
| M | 3.33 | 0.061 | 5 | 3.26 – 3.41 |
| F | 3.42 | 0.028 | 2 | 3.17 – 3.67 |
| | | Width across upper molars | | |
| M | 5.58 | 0.125 | 5 | 5.43 – 5.74 |
| F | 5.61 | 0.120 | 2 | 4.52 – 6.69 |
| | | Length of maxillary toothrow | | |
| M | 5.77 | 0.142 | 5 | 5.60 – 5.95 |
| F | 5.62 | 0.085 | 2 | 4.86 – 6.38 |
| | | Length of mandibular toothrow | | |
| M | 6.16 | 0.190 | 5 | 5.92 – 6.39 |
| F | 6.14 | 0.064 | 2 | 5.56 – 6.71 |

TABLE 9.—*Continued.*

| Sex | Mean | SD | N | CI |
|---|---|---|---|---|
| | | Percent reflectance of red | | |
| M | 16.4 | 2.72 | 5 | 13.02 – 19.78 |
| F | 18.3 | 1.06 | 2 | 8.72 – 27.78 |
| | | Percent reflectance of green | | |
| M | 8.5 | 0.935 | 5 | 7.34 – 9.66 |
| F | 8.8 | 0.354 | 2 | 5.57 – 11.92 |
| | | Percent reflectance of blue | | |
| M | 7.0 | 1.173 | 5 | 5.54 – 8.46 |
| F | 8.3 | 0.354 | 2 | 5.08 – 11.43 |

distance algorithm was used in this analysis. Resulting dendrograms, in which males and females were pooled, from these analyses are presented in Fig. 6.

One other proposed name, *Myotis micronyx,* which was placed in synonymy of *M. evotis* by Miller and Allen (1928), is known from a single specimen from Comondú. The identity of this bat as a representative of *evotis* has been verified by several people (for example, Barbour and Davis, 1969; J. K. Jones, Jr., personal communication). I have not personally examined this specimen, but I took published measurements from the original description and ran a discriminant function analysis using an abbreviated suite of characters (for example, no color reflectance readings were available to me for *micronyx*). On the basis of length of forearm and several cranial measurements, this individual was classified with material from the Pacific Northwest (PACNW) and not with material from southern California (SOCAL) or northeastern Baja California (BAJAM, *milleri*), its nearest geographic

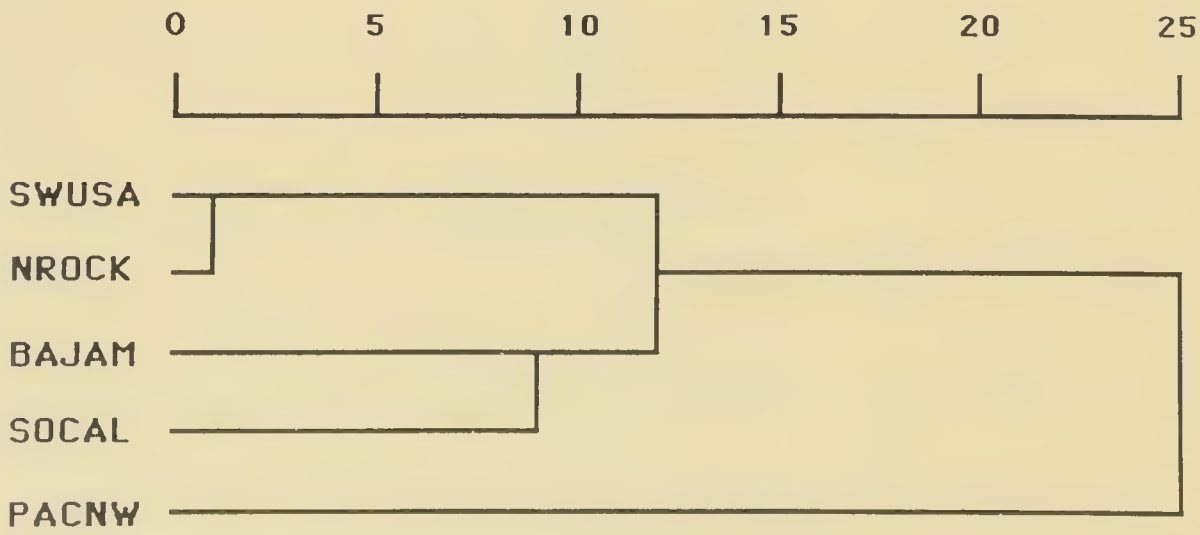



FIG. 6.—Dendrograms produced by cluster analysis (UPGMA, Euclidean distance) of mean values of 15 dependent variables, sexes combined, in sample groups one to four and *milleri* from Baja, California, México. Horizontal bar indicates rescaled morphometric differences between groups.

neighbors. Because it is known from only one specimen, it was excluded from further statistical analyses.

In summary, my analyses indicate that six subspecific taxa of long-eared myotis should be recognized at this time (each of the four reconstituted groups north of México and two isolated races from Baja, California) as follows: *M. e. evotis* (SOCAL), a small, pale race from the southern coastal ranges and adjacent areas of California; *M. e. chrysonotus* (NROCK), a medium-sized, pale subspecies from northern and interior Rocky Mountain areas and adjacent plains to the east; an undescribed subspecies (SWUSA), which is a large and moderately pale bat from western New Mexico and the northern part of Arizona; *M. e. pacificus* (PACNW), a small, dark race from coastal areas of northern California, Oregon, Washington, and southern Bristish Columbia; *M. e. milleri* (BAJAM), a small pale, relictual taxon, restricted to Sierra San Pedro Mártir, Baja California; and *M. e. micronyx*, a relatively small bat of medium dark color, known only from Comondú, Baja California Sur, which is recognized only tentatively pending acquisition of additional material. The single specimen from Comondú, which represents the holotype of *Myotis micronyx*, and the population known as *milleri*, which recently was reviewed and treated as a distinct species by Reduker *et al.* (1983), are discussed in the accounts of subspecies. Additional specimens from elsewhere within the range of the species that comprise small samples or represent intermediate and outlying areas with reference to the four major groups are discussed in these accounts as well (see specimens examined and map showing distribution of these taxa).

## Accounts of Subspecies

### *Myotis evotis* (H. Allen, 1864) (synonymy under subspecies)

*Distribution.*—The long-eared myotis, *Myotis evotis*, is found in temperate western North America from southern British Columbia, Saskatchewan, and Alberta, south through Washington, Oregon, and California to Baja California. Inland it occurs eastward through Idaho and Montana to extreme western North Dakota and northwestern South Dakota, hence southward through Wyoming and western Colorado to New Mexico, northern Arizona, Utah, and Nevada (see Fig. 7). This species is known to occur from near sea level along the Pacific Coast to about 2800 meters in Wyoming (Manning and Jones, 1989).

*Description.*—One of the largest species of the American long-eared myotis group, both externally and cranially; ears long (when laid forward extending 5 mm or more beyond tip of nose); heavily pigmented; calcar lacks definite keel; posterior border of uropatagium lacks conspicuous fringe (may be slightly ciliate in some individuals); pelage long, glossy, with individual hairs of dorsum dark basally; forearm length ranging from about 35 to 41, usually less than 40 (depending on subspecies); toothrows long, premolars in line, not crowded, molars relatively

robust; auditory bullae large when compared to those of other closely related species. As in most other members of the genus, the dental formula is: i 2/3, c 1/1, p 3/3, m 3/3, total 38. Karyotypically, *M. evotis* has a diploid number of 44 and fundamental number 52. The Y chromosome is large, composed mostly of heterochromatic material (Bickham, 1979; Baker and Bickham, 1980).

*Remarks.*—As mentioned previously, nowhere is *Myotis evotis* especially common, and large series of specimens from a single locality are lacking over much of the known distribution of the species. Frequently, I had single specimens, or only a few specimens (often partial material, skins alone or skulls only, for example), from broad geographic areas. Therefore, the exact boundaries between adjacent subspecies were not always easy to delineate; in some cases, specimens available from such areas appeared to be intermediates. These apparent distributional gaps or areas of intergradation are mentioned in the accounts of subspecies.

Pelage color is a valid criterion for identification to subspecies for only one of the known races (*pacificus*); I found no significant difference in color of pelage between other races, all of which are generally pale. A combination of external and cranial characters proved most reliable when considering subspecific identity among the pale-colored subspecies.

It long has been recognized that two subspecies of *M. evotis* are found in British Columbia. However, no modern study of geographic variation has been undertaken to delineate subspecific boundaries there (Nagorsen, 1990), and Canadian material, unfortunately, was limited to a single specimen for my study. In the most recent systematic inquery involving species of long-eared myotis from Canada (van Zyll de Jong, 1979), members of both "dark" and "pale" races were pooled when compared with two other long-eared species (*M. keenii* and *M. septentrionalis*). It was, therefore, difficult for me to assign specimens to subspecies based on van Zyll de Jong's work. Thus, I have relied primarily on earlier published records and descriptions, but the exact distributional limits of subspeces of *evotis* in Canada probably cannot be resolved with the relatively few specimens available for analysis at this time.

### *Myotis evotis evotis* (H. Allen)

1864. *Vespertilio evotis* H. Allen, Smithsonian Misc. Coll., 165: 40.
1897. *Myotis evotis* Miller, N. Amer. Fauna, 13: 1897:77.

*Type material.*—None identified specifically in the orignal description. Lectotype designated by Lyon and Osgood (1909) as USNM 5389, sex unknown, preserved in alcohol; obtained by A. S. Taylor, but no original number or collection date recorded; catalogued on 31 October 1861 (lectotype not now to be found—Lyon and Osgood,1909). Type locality restricted to Monterey, Monterey Co., California by Miller (1897:40, 77).

*Distribution*.—Inland areas surrounding San Fransisco Bay southward throughout the Coastal Range of southern California to San Diego County, (Fig. 7).

*Description*.—A relatively small race of the long-eared myotis characterized by pale-colored pelage and heavily pigmented ears and membranes. Pelage of middorsal region approximately 8 to 10 mm in length, distal 5 to 6 mm of each hair with rich brownish-golden color, black basally. Forearm moderately short for the species (approximately 34.6 to 36.3), greatest length of skull ranging from about 15.2 to 15.6. Representative external measurements are given in Table 10; length of forearm, cranial measurements, and color-reflectance readings are in Table 6.

Average zygomatic breadth (not used in analyses) of 13 males and 14 females (extremes in parentheses) from Group 2 (SOCAL) was 9.0 (8.5–9.3) and 9.2 (8.7–9.5), respectively. Average weight of four males and five females from this same sample was 5.3 (4.2–6.0) and 5.6 (4.3–6.3), respectively.

*Comparisons*.—From *Myotis evotis pacificus*, the relatively small and darkly colored subspecies that occurs in coastal regions to the north, *M. e. evotis* differs as follows: coloration paler throughout, contrast between pelage and membranes much more noticeable; size slightly smaller externally (forearm averaging less than, not more than, 36—see Table 10); crania essentially equal in size, except that of *pacificus* significantly broader across upper canines (see Table 6).

From inland populations representing *Myotis evotis chrysonotus* to the northeast and a new subspecies described beyond, which occurs in Arizona and New Mexico, *M. e. evotis* differs in being smaller, both externally and cranially (see Tables 6 and 10), significantly so in most measurements. The two inland races also are slightly paler than *evotis*.

*Myotis evotis micronyx* and *M. e. milleri* of Baja California are disjunct races that are not in contact with *evotis* or each other as their distributions are currently understood. From *M. e. milleri*, the subspecies *evotis* differs principally in being larger in size and in having a slightly more flattened braincase. From *M. e. micronyx*, known only from the holotype, there are few demonstrable differences, although the considerable distance between the southern edge of the known range of *evotis* and the type locality of *micronyx* (Comondú, Baja California Sur), with *milleri* juxtaposed in between, argues for nomenclatorial recognition of this population, at least until more and better data are available. Based on the holotype, *micronyx* may have a somewhat smaller, narrower skull than typical *evotis*.

*Remarks*.—Miller (1897), acting as first revisor, restricted the type locality of *M. e. evotis* to Monterey, California. He did not, however, designate a lectotype. Lyon and Osgood (1909:209) accepted Miller's (1897:77) statement that "Monterey, Cal. (one of the localities given), may be selected as the type locality" and designated as lectotype USNM 5389, the only specimen listed in the original description from Monterey. Unfortunately, however, no specimen labeled as 5389 then could be found in the national collection according to Lyon and Osgood

TABLE 10.—*Descriptive statistics for external measurements for samples of* Myotis evotis *(sexes reported separately) for groups 1, 2, 3, 4, and 5 (BAJAM). Abbreviations used; SD (standard deviation), N (sample size), and CI (95 percent confidence interval).*

| Group | Mean | SD | N | CI |
|---|---|---|---|---|
| | | Length of forearm | | |
| Males | | | | |
| 1 PACNW | 36.3 | 1.30 | 21 | 35.68 – 36.86 |
| 2 SOCAL | 35.3 | 1.37 | 19 | 34.68 – 35.99 |
| 3 NROCK | 38.2 | 1.00 | 53 | 37.97 – 38.52 |
| 4 SWUSA | 39.2 | 0.95 | 95 | 39.03 – 39.42 |
| 5 BAJAM | 34.2 | 1.06 | 6 | 33.09 – 35.31 |
| Females | | | | |
| 1 PACNW | 36.8 | 1.14 | 29 | 36.32 – 37.19 |
| 2 SOCAL | 35.8 | 1.02 | 16 | 35.24 – 36.33 |
| 3 NROCK | 38.6 | 1.38 | 38 | 38.26 – 38.90 |
| 4 SWUSA | 40.0 | 1.13 | 85 | 39.74 – 40.22 |
| 5 BAJAM | 35.3 | 0.23 | 2 | 33.26 – 37.32 |
| | | Total length | | |
| Males | | | | |
| 1 PACNW | 87.8 | 5.34 | 20 | 85.25 – 90.25 |
| 2 SOCAL | 88.1 | 4.28 | 17 | 85.86 – 90.26 |
| 3 NROCK | 91.7 | 4.70 | 50 | 90.40 – 93.08 |
| 4 SWUSA | 92.4 | 4.00 | 79 | 91.46 – 92.25 |
| 5 BAJAM | 88.2 | 4.92 | 6 | 83.01 – 93.33 |
| Females | | | | |
| 1 PACNW | 89.0 | 4.21 | 28 | 87.37 – 90.63 |
| 2 SOCAL | 86.4 | 3.37 | 16 | 84.64 – 88.23 |
| 3 NROCK | 90.5 | 4.97 | 40 | 88.86 – 92.04 |
| 4 SWUSA | 93.6 | 4.21 | 80 | 92.65 – 94.52 |
| 5 BAJAM | 85.5 | 4.95 | 2 | 41.03 – 129.97 |
| | | Length of tail vertebrae | | |
| Males | | | | |
| 1 PACNW | 39.0 | 3.08 | 20 | 37.56 – 40.44 |
| 2 SOCAL | 40.7 | 3.67 | 17 | 38.76 – 42.54 |
| 3 NROCK | 41.7 | 2.93 | 50 | 40.87 – 42.53 |
| 4 SWUSA | 41.4 | 2.37 | 79 | 40.90 – 41.96 |
| 5 BAJAM | 40.8 | 3.25 | 6 | 37.42 – 44.24 |
| Females | | | | |
| 1 PACNW | 39.1 | 3.15 | 28 | 37.92 – 40.36 |
| 2 SOCAL | 40.6 | 2.16 | 16 | 39.41 – 41.71 |
| 3 NROCK | 41.4 | 2.98 | 40 | 40.47 – 42.38 |
| 4 SWUSA | 42.0 | 2.60 | 80 | 41.45 – 42.60 |
| 5 BAJAM | 39.0 | 0.00 | 2 | 39.00 – 39.00 |

TABLE 10.—*Continued.*

| Group | Mean | SD | N | CI |
|---|---|---|---|---|
| | | Length of hind foot | | |
| Males | | | | |
| 1 PACNW | 9.5 | 1.31 | 15 | 8.87 – 10.20 |
| 2 SOCAL | 9.0 | 1.08 | 14 | 8.34 – 9.59 |
| 3 NROCK | 9.2 | 1.01 | 50 | 8.94 – 9.51 |
| 4 SWUSA | 8.8 | 1.12 | 79 | 8.56 – 9.06 |
| 5 BAJAM | 8.8 | 1.33 | 6 | 7.44 – 10.23 |
| Females | | | | |
| 1 PACNW | 9.3 | 0.68 | 28 | 9.04 – 9.57 |
| 2 SOCAL | 9.0 | 1.31 | 11 | 8.07 – 9.84 |
| 3 NROCK | 9.1 | 1.32 | 40 | 8.63 – 9.47 |
| 4 SWUSA | 9.1 | 1.03 | 80 | 8.87 – 9.32 |
| 5 BAJAM | 8.5 | 0.71 | 2 | 2.15 – 14.85 |
| | | Length of ear | | |
| Males | | | | |
| 1 PACNW | 20.7 | 1.33 | 14 | 19.95 – 21.48 |
| 2 SOCAL | 21.2 | 1.58 | 18 | 20.41 – 21.98 |
| 3 NROCK | 21.1 | 1.33 | 50 | 20.68 – 21.44 |
| 4 SWUSA | 21.5 | 1.92 | 78 | 21.09 – 21.95 |
| 5 BAJAM | 20.3 | 1.21 | 6 | 19.06 – 21.60 |
| Females | | | | |
| 1 PACNW | 19.7 | 1.70 | 27 | 19.03 – 20.38 |
| 2 SOCAL | 22.3 | 1.69 | 15 | 21.37 – 23.22 |
| 3 NROCE | 21.1 | 1.42 | 34 | 20.60 – 21.59 |
| 4 SWUSW | 21.6 | 1.82 | 80 | 21.24 – 22.05 |
| 5 BAJAM | 20.5 | 0.71 | 2 | 14.15 – 26.85 |

(1909). To my knowledge, the specimen never has been located. Later, Poole and Schantz (1942) interpreted H. Allen's (1894) comment concerning a specimen from Easton, Washington, which he regarded as "typical *evotis*," as defining the dark-colored race now known as *pacificus* as the subspecies *evotis*, and they selected a specimen from Puget Sound (according to them, one of the bats from original description) as the lectotype. This specimen, USNM 5391/38660, preserved in fluid with skull removed, was then in the collection (Poole and Schantz, 1942:152). Because Miller (1897) already had fixed the type locality, their action was invalid. Dalquest (1943) followed Lyon and Osgood (1909) and Miller (1897) when he confirmed restriction of the type locality of *M. e. evotis* to Monterey, Monterey Co., California, and named the dark-colored race as *M. e. pacficus*.

In the interest of nomenclatorial stability and common sense, I think it only appropriate to confirm Monterey, Monterey Co., California, as the type locality of the

pale-colored *evotis* of the California coast, following reasons given by Miller (1987), Lyon and Osgood (1909), and Dalquest (1943).

*Specimens examined.*—Total of 43 as follows. California. *Alameda Co.*: Calaveras Dam, 1 (MVZ). *Colusa Co.*: 2.5 mi. N Goat Mountain Lookout, Summitt Valley, 1 (MVZ). *Contra Costa Co.*: Howard Ranch, 10 mi. E Clayton, 1 (MVZ). *Lake Co.*: *Lucerne, Clear Lake*, 1 (MVZ). *Los Angeles Co.*: San Antonio Canyon, San Gabriel Mts., 12 (KU); Big Santa Anita Canyon, near Pasadena, 1 (MVZ); Arroyo Seco Canyon, near Pasadena, 1 (MVZ). *Monterey Co.*: Lewis Creek, Diablo Range, 2 (MVZ); *Priest Valley, Diablo Range*, 1 (MVZ); *Arroyo Seco (Abbot Ranch House)*, 1 (MVZ). *Napa Co.*: Aetna mines, 1 (MVZ). *San Diego Co.*: *Hubbards Grove Bridge*, 1 (KU); Cuyamaca State Park, 1 (KU); *Cuyamaca Rancho State Park, Paso Picacho Campground*, 3 (HSU), 3 (MVZ); *Campfire Girls Swimming pool, Cuyamaca Mts.*, 1 (MVZ); Palamar Mountain, 1 (MVZ); *Doane Valley, Palomer Mt.*, 1 (MVZ). *San Bernadinio Co.*: San Bernadino Mountatins, 2 (USNM). *San Luis Obispo Co.*: 5 mi. SSW Adelaida, 1 (MVZ). *Santa Barbara Co.*: Santa Barbara School, 1 (MVZ). *Santa Clara Co.*: Halls Valley, Mount Hamilton, 1 (MVZ). *Santa Cruz Co.*: fork of Waddell Creek, 4 (MVZ).

*Selected additional records.*—California. Santa Catalina Island; *Santa Cruz Island.* According to Hall (1981:208), these insular specimens originally were reported simply under the specific name *Myotis evotis* by von Bloeker (1967:248).

## *Myotis evotis chrysonotus* (J. A. Allen)

1896. *Vespertilio chrysonotus* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 8:240.
1928. *Myotis evotis chrysonotus* Miller and Allen, Bull. U. S. Nat. Mus., 144:116.

*Type material.*— Adult female, skin only, AMNH 11645; obtained on 21 July 1895 by W. W. Granger, original no. not reported. Type locality Kinney Ranch, Bitter Creek, Sweetwater Co., Wyoming. Type specimen not examined.

*Distribution.*—Northern and interior parts of western United States, including parts of southeastern Oregon, inland areas of northern and central (Sierra Nevada) California, southern Idaho, Nevada, Utah, central and eastern Montana, extreme western North and South Dakota, Wyoming, Colorado, and north-central New Mexico; also found in adjacent Canadian provinces of Alberta, British Columbia, and Sasketchewan (Fig. 7).

*Description.*—A medium-sized race of long-eared myotis characterized by pale-colored pelage, heavily pigmented ears, and moderately heavy pigmented flight membranes. Pelage of middorsal region approximately 8 to 10 mm in length, the distal 5 to 6 mm of each hair with rich golden (buffy-straw) color, making this the palest of known subspecies; hairs black basally. Forearm moderately long, approximately 37.9 to 38.9; greatest length of skull varies from about 15.9 to 16.1. Representative external measurements are given in Table 10; length of forearm, cranial measurements, and color reflectance readings for pelage are presented in Table 6.

Average zygomatic breadth (not used in analyses) of 41 males and 32 females (ranges in parentheses) from the northern Rocky Mountains area (Group 3, NROCK) was 9.45 (8.95–9.98) and 9.50 (8.97–10.12), respectively. Average

weight of 37 males and 26 females from the same group was 6.6 (4.9–9.5) and 6.7 (4.7–9.1), respectively.

*Comparisons.*—For comparisons with the nominate subspecies of coastal California, see that account. From bats occurring in Arizona and New Mexico, described as a new subspecies in the next account, *M. e. chrysonotus* differs as follows: color of middorsal pelage slightly paler, with slightly more contrast between ears and flight membranes; size smaller externally (forearm less than, not greater than, 39—see Table 10); skull smaller and narrower, significantly so in nearly all dimensions including GLS, CBL, MB, RL, CC, M3M3, MTR, and CM3 (see Table 6).

This race (*M. e. chrysonotus*) from interior areas of the Rocky Mountains differs from two isolated populations in Baja California, *M. e. milleri*, and *M. e. micronyx*, in being larger both externally (forearm greater than, not less than, 37.5); cranium larger in nearly all measurements (for example, GLS greater than, not less than, 15.8).

From *Myotis evotis pacificus* of the Pacific Northwest, *chrysonotus* is paler, significantly different in all three color (red, green, and blue) reflectance readings, giving a sharp contrast between pelage and flight membranes and ears; size externally slightly larger (forearm length greater than 37.5); crania significantly larger and broader in most dimensions including GLS, CBL, MB, RL, DBC, CC, MTR, and M3M3 (see Table 6).

*Remarks.*—Available specimens from northern California and the Sierra Nevada range are slightly darker in color and slightly smaller externally and cranially, on average, than are bats from interior areas of the Rocky Mountains.

Long-eared myotis from several counties in California (Calaveras, El Dorado, Fresno, Kern, Lassen, Modoc, Placer, Shasta, Sierra, Tehema, and Toulumne) and southwestern Nevada (Clark, Mineral, and Nye) appear to be intermediate between the relatively small coastal subspecies (*evotis*) and the medium-sized inland race (*chrysonotus*). One real problem in analyzing material from this region is the paucity of specimens (less than 20) available for study. Discriminant function analysis classified specimens, entered as unknowns, from the entire region as follows: approximately 13 percent to *pacificus*, 37 percent to *evotis*, 25 percent to *chrysonotus*, and 25 percent to the larger southwestern race named beyond. No distinct pattern, or geographic correlate, was apparent when examining the specimens. Those from the southern part of the area tend to be somewhat smaller, pale-colored bats, like *evotis*, whereas specimens from northern areas are more darkly pigmented, approaching *pacificus*, in color.

When examined and treated as one group (there are no apparent physiographic barriers between sample localities), the following average external, cranial, and color readings resulted: length of forearm, 37.4 ($N$=15); greatest length of skull, 15.4 ($N$=13); and percent reflectance of red, 14.6 ($N$=15). Linear measurements are

larger than those of coastal subspecies (*pacificus* and *evotis*) of this species, and average only slightly smaller than those of *chrysonotus*. Color readings are intermediate (see Table 6 and Table 10 for comparartive cranial and external measurements) between *pacificus* and the small, pale-colored subspecies.

All specimens from the region in question are assigned tentatively to *M. e. chrysonotus* because they average only slightly smaller and only slightly darker than specimens from elsewhere in the distribution of that subspecies. Careful studies of additional series of specimens from this region should help to delineate either subspecific boundaries or to confirm the intermediate status of individuals from the rather broad zone of intergradation, as presently understood.

*Myotis evotis* had been reported from northwestern Nebraska (Jones, 1964) and southwestern South Dakota (Miller and Allen, 1928). Later, long-eared bats from this area were studied in more detail, and were found to represent a new subspecies of *Myotis thysanodes* (*pahasapensis*) that was described by Jones and Genoways (1967). Their study clearly demonstrated that long-eared bats from this region represented *thysanodes* and not *evotis*. Jones and Choate (1978) reviewed the status of these two taxa of long-eared bats (*evotis* and *thysanodes*) on the northern Great Plains.

Larrison and Johnson (1981:25) wrote that in Idaho both the "subspecies, *evotis* [=*chrysonotus*] and *pacificus* (a migrant only), have been taken in the state." Earlier, Davis (1939:114) had noted: "In Idaho, the race *chrysonotus* occurs in the southern portion of the state and ranges north as far as at least latitude 45 degrees N. Although no specimens of the closely allied, darker, coastal race *M. e. evotis [=pacificus]* have been recorded from Idaho, its occurrence in the northern part of the state is within the realm of geographic probability."

*Specimens examined.*—Total of 197 as follows. California. *Calaveras Co.*: 9 mi. E Murphy, 1 (MVZ); *El Dorado Co.*: Kings Meadow,1 (MVZ). *Fresno Co.*: 0.25 mi. SW Big Stump Fox Farm, near Grant National Park,1 (MVZ); *Kern Co.*: Rancheria Creek, 3 (KU ). *Lassen Co.*: *Clarks Valley,* 1 (MVZ); Black Mountatin Experimental Station, 1 (MVZ). *Modoc Co.*: Cedarville, 1 (MVZ). *Mono Co.*: Inyo National Forest, Taylor Canyon, 1 (HSU); Sweetwater Canyon, 1 (MVZ). *Nevada Co.*: Independence Lake,1 (MVZ). *Placer Co.*: Lake Tahoe, 0.5 mi. S Tahoe Tavern, 1 (MVZ). *Plumas Co.*: Rich Gulch, 8 mi. N, 11 mi. W Quincy, 1 (MVZ). *Shasta Co.*: Warner Creek, Lassen Peak, 2 (MVZ). *Sierra Co.*: Haskell Creek, Tohac National Park, 1 (MVZ); *0.2 mi. N, 3.2 mi. W Calpine*, 1 (MVZ). *Tehama Co.*: Antelope Creek, 5 mi. SE Lyonsville, 1 (MVZ); *Lassen Road, 2 mi. W Black Butte,* 2 (MVZ); Sisson, 1 (USNM). *Tuolumne Co.*: 1 mi. NE Mather, 1 (KU). Colorado. *Alamosa Co.*: 3 mi. N, 18 mi. E Mosca, Great Sand Dunes National Park, Denton Springs, 2 (MHP). *Archuleta Co.*: Deep Canyon, 3 (MSB); *Devil Creek*, 2 (UTEP). *Delta Co.*: 8 mi. NW Hotchkiss, Charles Grey Ranch, 1 (UCM). *Garfield Co.*: 28 mi. N Loma, Douglass Pass, 3 (UCM). *Gunnison Co.*: 4 mi. W Sapinero, 1 (KU). *Larimer Co.*: Loveland, 1 (USNM). *Las Animas Co.*: 4 mi. S, 3.75 mi. W Gulnare, 1 (MHP). *Mesa Co.*: 4 mi. NE Gateway, 1 (UCM); 4 mi. S, 3 mi. E Collbran, 1 (KU). *Moffat Co.*: *S Sunny Peak, [Little] Snake River*, 5 (USNM); 6 mi. SW Greystone, 4 (UCM); *5 mi. SE Elk Springs*,16 (UCM); 1 mi. SW Cross Mountain, 3 (KU). *Montezuma Co.*: Rock Springs, Mesa Verde National Park, 2 (KU); *Museum Headquarters, Mesa Verde National Park,* 1 (KU); *Ashbaugh Ranch,*1 (USNM). *Rio Blanco Co.*:

6 mi. SW Meeker, Hay Gulch Road, 1 (UCM). *Routt Co.*: Sand Mountain, 5 mi. NW Milner, 1 (UCM); *5 mi. E Oak Creek*, 1 (UCM). *Saguache Co.*: 3 mi. N, 6 mi. E Mineral Hot Springs,1 (MHP); *Valley View, Hot Springs*, 1 (MHP). Idaho. *Bannock Co.*: 9.5 mi. E Pocatello, West Fork Rapid Creek, Barrels Ranch, 1 (MVZ). *Butte Co.*: Great Owl Cavern, Crater of the Moons National Monument, 1 (MVZ). *Cassia Co.*: Albion, 2 (USNM). Montana. *Carter Co.*: 11.5 mi. N, 3 mi. E Ekalaka, 2 (KU); 7 mi. N, 10 mi. W Camp Crook, 7 (KU); *6.5 mi. N, 5.5 mi. W Camp Crook*, 1 (KU); *5 mi. N, 8 mi. W Camp Crook*, 2 (KU); *5 mi. N, 6 mi. W Camp Crook*, 1 (KU); *5 mi. N, 6 mi. W Camp Crook, West Plum Creek Reservoir*, 4 (KU); *2 mi. N, 4.5 mi. W Camp Crook*, 1 (KU). *Chouteau Co.*: Highwood Mountains, 1 (USNM). *Fergus Co.*: Big Snowy Mountains, 18 mi. S, 3 mi.W Lewistown, 1 (KU). *Granite Co.*: ghost town of Garnet, 1 (UMZ). *Judith Basin Co.*: 13 mi. W Buffalo, Buffalo Canyon, 2 (USNM). *Meagher Co.*: 4 mi. S Fort Logan, Camas Creek, Big Belt Mountains, 1 (USNM). *Powder River Co.*: Powderville, 1 (KU). Nevada. *Clark Co.*: Sheep Mountains, 1 (KU). *Elko Co.*: *Little Owyhee River*, 1 (USNM); 2 mi. S, 7.75 mi. W Haystack Ranch, 1 (MHP); Goose Creek (approx. 2 mi. W Utah line), 1 (MVZ); Jarbridge, 1 (MVZ); *east side Spruce Mountain*, 2 (MVZ). *Eureka Co.*: Diamond Valley, 4 mi. S Romano, 1 (MVZ). *Mineral Co.*: Cottonwood Creek, Mount Grant, 1 (MVZ). *Nye Co.*: Quinn Canyon Mountains, Burned Corral Canyon, 1 (MVZ); Hot Creek Range, 7 mi. W Tyho, 1 (MVZ). *White Pine Co.*: Willow Creek, 2 mi. S White Pine County Line, Ruby Mts., 1 (KU); Mount Moriah, 2 mi. W Smith Creek Cave, 1 (MVZ). New Mexico. *Colfax Co.*: 17 mi. NW Cimarron, Philmont Scout Ranch, 6 (MSB). *Rio Arriba Co.*: 4 mi. N, 9 mi. E Canjilon, 3 (MSB); *1 mi. W Burford Lake*, 2 (MSB); *12 mi. S Canjilon, Yeso Tank*, 2 (KU). *San Juan Co.*: 1mi. S, 8 mi. W Sheep Spring, Chuska Mts., 1 (MSB). *Taos Co.*: 6.5 mi. N,1.5 mi. E Questa, Rio del Medio, 1 (MSB); *6 mi. N, 1 mi. E Questa, Rio del Medio*, 1 (MSB); *T22N, R13E, NW 1/4 sec 24 [ NE of Questa]*, 4 (MSB). *Union Co.*: 3 mi. N Capulin, West base Capulin Mt., 3 (MWSU); *4 mi. N Capulin*,1 (MWSU). North Dakota. *Billings Co.*: 1 mi. S,1 mi. W Medora, 1(KU). *Dunn Co.*: 5 mi. N, 6.5 mi. W Killdeer, 1 (KU). *Williams Co.*: 4 mi. W Grinnell, 1 (USNM). Oregon. *Harney Co.*: 1 mi. SE Blitzen Crossing Campground, Steens Mountains, 2 (PSMNH); *Steens Mountains*, 1 (OSUFW). *Malheur Co.*: Cottonwood Creek, 8 (PSMNH). South Dakota. *Harding Co.*: 10 mi. N, 5 mi. W Reva, 14 (KU); 7 mi. S, 4.5 mi. E Reva, 1 (KU); *NW 1/4 sec. 15, R5E, T22N* , 2 (KU); 5 mi. N, 2 mi. W Camp Crook, 1 (KU). Utah. *Piute Co.*: 0.5 mi. N, 1.5 mi. E Greenwich, 2 (UTEP). *San Juan Co.*: 13 mi. SW Monticello, 4 (MWSU); *10 mi. WSW Monticello, Indian Creek*, 3 (MWSU); North Notch Spring, Elk Mountains, 1(MSB); *Elk Ridge, Round Mountain*, 1 (MSB); *Indian Creek, Blanding, Monticello road, over Abajo Mtns.*, 1(MSB); 6 mi. N Blanding,1 (MSB); *3 mi. N Blanding*,1 (MSB). Wyoming. *Bighorn Co.*: Paint Rock Creek, 3 mi. E Hyatt Ranch,1 (USNM). *Carbon Co.*: Bottle Creek Picnic Ground, Sierra Madre Mts., 2 (KU). *Park Co.*: 15 mi. S, 21 mi. W Cody, 1 (KU). *Sublette Co.*: 6 mi. N, 3 mi. E Pinedale, 1 (KU). *Sweetwater Co.*: Kinney Ranch, approx. 23 mi. SW Bittercreek,1 (MVZ). *Teton Co.*: 4 mi. NNE Blacktail Butte,1 (MSB); *2 mi. N Blacktail Butte*, 1 (MSB). *Uinta Co.*: Fort Bridger, 1 (MVZ).

*Selected additional records.*—Alberta. vicinity of Rumsey (Soper, 1965:91). British Columbia. Smithers (van Zyll de Jong, 1985:98; Summit Lake, Near Prince George (van Zyll de Jong, 1985:98); Cranbrook (Cowan and Guiguet, 1960:80). Saskatchewan. Matador field station, near Matador; 26 km S Bengough (van Zyll de Jong, 1985:98). Colorado. (Armstrong,1972:61): *Boulder Co.*: Boulder. *Douglas Co.*: Daniels Park. *El Paso Co.*: 3 mi. N Colorado Springs. *Huerfano Co.*: *12.5 mi. W Gardner. Larimer Co.*: *14 mi. W Fort Collins*. Nevada. (Hall, 1946:138), unless otherwise noted. *Clark Co.*: *Clark Canyon; Lee Canyon; Kyle Canyon. Humboldt Co.*: Summit Lake road. *Lander Co.*: Kingston Ranger station; *Peterson Creek, Shoeshone Mts. Lincoln Co.*: Pahranagat Valley (Miller and Allen, 1928:117). New Mexico. *Colfax Co.*: *Vermejo River* (Findley *et al.*, 1975:36). *Rio Arriba Co.*: *Ghost Ranch, 12 mi. NW*

*Abiquiu* (Constantine, 1961:93). *San Miguel Co.*: *Sapello Canyon* (Miller and Allen, 1928:117). UTAH (records from Durrant, 1952:43, unless otherwise noted). *Uintah Co.*: 2 mi. above White River (Krutzsch and Heppenstall, 1955:126); *Willow Creek, 25 mi. S Ouray. San Juan Co.*: Verdure. *Washington Co.*: Zion National Park; St. George (Hardy, 1941:290. WYOMING. *Fremont Co.*: Bull Lake (Miller and Allen, 1928:118). *Laramie Co.*: Laramie County only (Clark and Stromberg, 1987:53). *Weston Co.*: 1.5 mi. S Buckhorn (Long, 1965:532). *Teton Co.*: *Jackson Hole* (Findley,1954:434).

### *Myotis evotis jonesorum*, new subspecies

*Type material*.— Holotype is an adult female, skin and skull, The Museum, Texas Tech University, 60269 (formerly Museum of Southwestern Biology, Albuquerque, New Mexico, 5101), from Bear Trap Canyon, 20 mi. S, 19 mi. W Magdalena, San Mateo Mountains, Socorro Co., New Mexico; obtained on 29 July 1958 by A. H. Harris, original no. 1185.

External measurements and weight (taken from specimen label except for length of forearm) of the holotype are: total length, 91; length of tail, 41; length of hind foot, 9; length of ear, 22; length of forearm, 40.1; weight, 7.2 grams. Selected cranial measurements of the holotype are: greatest length of skull, 16.8; condylobasal length, 16.0; postorbital constriction, 3.9; zygomatic breadth, 9.8; mastoid breadth, 8.1, breadth of braincase, 7.3; length of rostrum, 7.6; depth of braincase, 5.3; width across upper canines, 4.1; width across upper molars, 6.3; length of maxillary toothrow, 6.4; length of mandibular toothrow, 6.9. Color-reflectance readings for the holotype are: R, 17.0; G, 8.5, and B, 8.5.

*Distribution*. —Kaibab Plateau of northern Arizona and Mogollon Rim (Colorado Plateau) of northeastern Arizona and western New Mexico (Fig. 7).

*Description*.—Largest, both externally and cranially, of the known subspecies of long-eared myotis. Pelage color slightly darker than in *chrysonotus*, best appreciated in direct comparison of large series of specimens. External measurements are given in Table 10; length of forearm, cranial measurements and color reflectance readings for pelage are presented in Table 6.

Average zygomatic breadth (not used in analyses) of 68 males and 65 females (extremes in parentheses) from the southwestern United States (Group 4, SWUSA) was 9.76 (9.09–10.53) and 9.87 (9.10–10.55), respectively. Average weight of 51 males and 59 females (extremes in parentheses) from the southwestern United States (Group 4, SWUSA) was 6.7 (4.8–8.9) and 7.2 (4.5–9.6), respectively.

*Comparisons*.—This is the largest of the known races. For comparartive differences between this subspecies and *M. e. evotis*, and *M. e. chrysonotus*, see those accounts. From *micronyx* and *milleri* from Baja California, this taxon is noticeably larger externally (forearm greater than 39 in *jonesorum*, whereas forearm length is less than 36.5 mm in both Mexican taxa); skull much longer, broader and deeper, larger in all measurements, easily separated by GLS (greater than 16.2 in *jonesorum*, less than 15.5 in both relictual populations).

From the much darker-pelaged *M. e. pacificus*, this newly described taxon is significantly paler in all color reflectance readings; size larger externally as demonstrated by length of forearm (greater than 39 mm in *jonesorum*, less than 37.2 mm in *pacificus*); skull larger in nearly all measurements, noteably GLS, CBL, MB, RL, M3M3, MTR, and CM3 (see Table 6).

*Remarks.*—The specific epithet, *jonesorum*, is a patronym for Clyde Jones and J. Knox Jones, Jr., my mentors.

Some specimens from the Jemez Mountains (Sandoval County, New Mexico) are intermediate in size, both externally and cranially, between this and the pale-colored inland race *chrysonotus*. Discriminant function analysis classified seven of 13 specimens (treated as unknowns) as belonging to this race; the others were classified as representing *chrysonotus*. Examination of other specimens from the region (for example, fluid specimens and a skull alone) suggest that bats from this area represent the larger of the two subspecies, and they are here tentatively assigned to *M. e. jonesorum*.

Hoffmeister (1986) mentioned two long-eared myotis, as "winter records" from Santa Cruz County, Arizona, near the Mexican border. He went on to state: "The winter records from the upper end of Madera Canyon, Santa Rita Mts., based on two specimens banded and released, could have been *M. auriculus*" (Hoffmeister, 1986:77). Because it is more than likely that these bats were in fact representatives of the southwestern myotis, the record is not admitted here.

*Specimens examined.*—Total of 261 as follows. Arizona. *Apache Co.*: Springerville, 1 (USNM); 4 mi. S, 16 mi. W Springerville, White Mts., 2 (MSB). *Coconino Co.*: *0.8 mi. NW Southwest Forest Experiment Station*, 1 (USNM); 3 mi. NW Flagstaff, ramada of Museum of Northern Arizona, 1 (MNA); 0.5 mi. S of north entrance Grand Canyon National Park, 2 (UIMNH); *North Rim GCNP, 2 mi. N Bright Angel Ranger Station, CCC camp*, 1 (UIMNH); *North Rim GCNP, Greenland Lake*, 4 (UIMNH); *campground near Neal Spring, north side Grand Canyon*, 4 (UIMNH); *old CCC area overlooking Kaibab Trail, GCNP*, 1 (UIMNH); *8.5 mi. N North Rim Ranger Station, GCNP*, 5 (MNA); *3.1 mi. N North Rim Ranger Station, Harney Pond, GCNP*, 5 (MNA); *3 mi. NW North Rim Ranger Station*, 10 (MNA); *4.8 mi. N, 8.5 mi. W North Rim Headquarters, Kanabonits Spring, GCNP*, 1 (MNA); *Murray Lake, 7.4 mi. S Jacob Lake*, 2 (MNA). New Mexico. *Catron Co.*: 9 mi. E Mogollon, Mogollon Mts., 4 (MSB), 1 (MHP), 1 (KSC); 2 mi. NE Wall Lake, Black Range, Taylor Creek, 1 (MSB); *10 mi. E Mogollon*, 6 (TTU); 10 mi. S Mogollon, 2 (TTU). *Sandoval Co.*: Rio Las Vacas, Jemez Mts., 8200 ft., 1 (MSB); 9 mi. S, 6 mi. W Los Alamos, Cochita Canyon, 4 (MSB); *T18N, R4E, SE 1/4 sec. 4 [near Cochita Canyon]*, 1 (MSB); *3.5 mi. S, 16.5 mi. W Los Alamos*, 3 (MSB); Bluebird Mesa, Jemez Mts., 10 (MSB); *5 mi. S, 15 mi. W Los Alamos, Los Conchas Campground*, 2 (MSB); *East Fork Jemez River*, 3 (MSB); Battleship Rock, 1 (MSB). *San Juan Co.*: Chuska Mts., 1 mi. S, 8 mi. W Sheep Spring, 1 (MSB). *Socorro Co.*: 20 mi. S, 19 mi. W Magdalena, Bear Trap Canyon, San Mateo Mts., 73 (MSB), 53 (MHP), 2 (KSC), 4 (TTU); *32 mi. S, 28 mi. W Socorro, Nagel Canyon, Weir Tank*, 9 (MSB); *32 mi. S, 19 mi. W Socorro, Springtime Campground*, 2 (TTU); *28 mi. S, 32 mi. W Socorro*, 1 (TTU); 10 mi. N, 5 mi. E Monticello, 6 (MSB); 38 mi. S, 6 mi. W Magdalena, Springtime Canyon, San Mateo Mts., 12 (MSB), 2 (TTU); *1.5 mi. E Springtime Canyon, San Mateo Mts., Weir Tank*, 6 (MSB); 14 mi. S, 3 mi. E Monticello, Springtime Canyon, 1 (MSB). *Valencia Co.*: *George Tank, Mt. Taylor*,

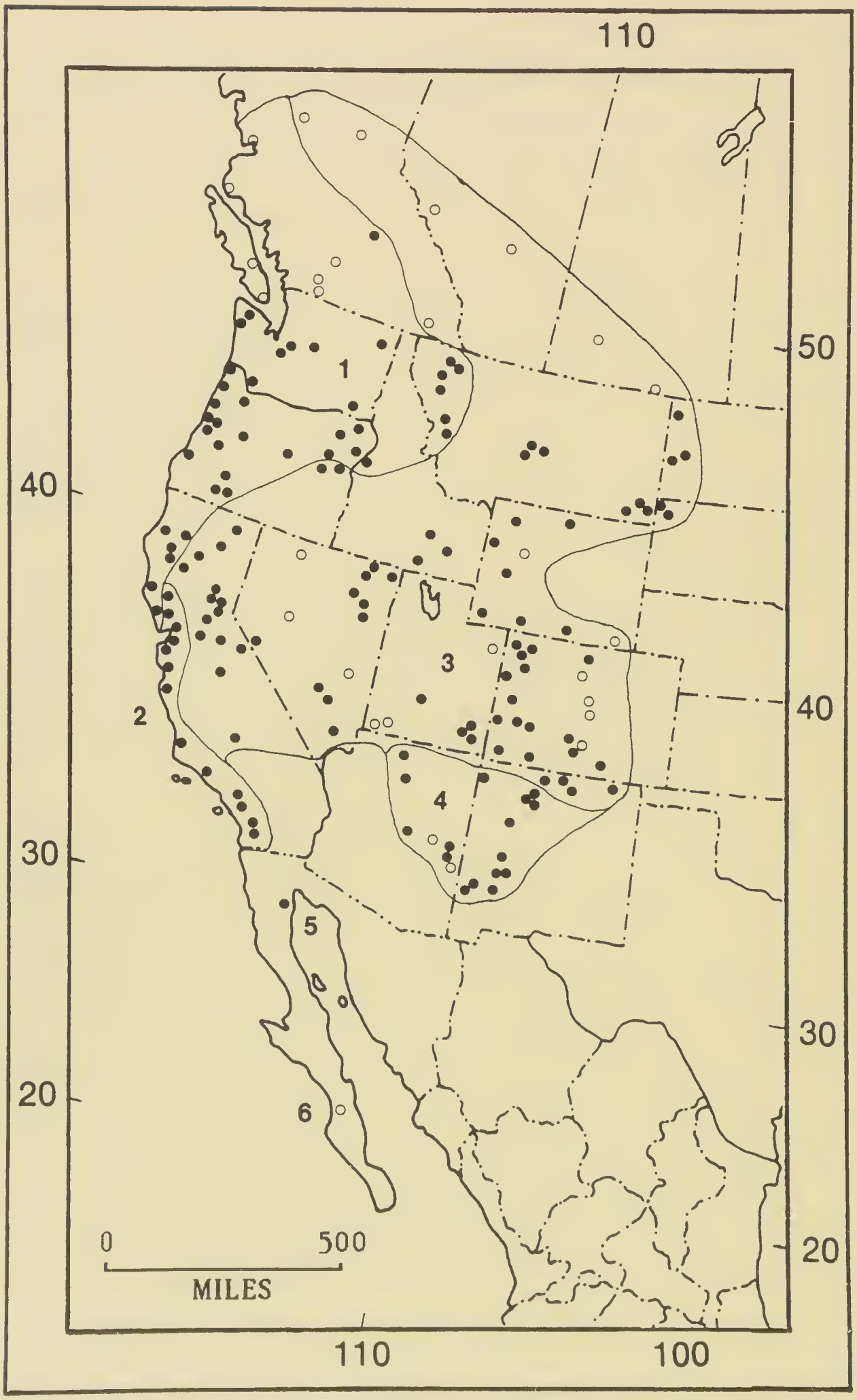



FIG. 7.—Map showing the distribution of six recognized subspecies of *Myotis evotis*. (1) *M. e. pacificus*; (2) *M. e. evotis*; (3) *M. e. chrysonotus*; (4) *M. e. jonesorum*; (5) *M. e. milleri*; and (6) *M. e. micronyx*.

2 (MSB); *4 mi. N, 17.5 mi. E Grants* , 1 (MSB); *17 mi. NE Grant, La Mosea Tank*, 1 (MSB); San Mateo Mountains, San Mateo Canyon, Mt. Taylor Range, 4 (MSB); *Mirabal Spring, Mt. Taylor*, 2 (MSB).

*Selected additional records.*—Arizona. *Greenlee Co.*: K. P. Cienega, 4 mi. S Hanagan Meadows (Hoffmeister, 1986: 78). *Navajo Co.*: Cooley's Ranch, White Mts. (Koopman, 1963:2). New Mexico. (Findley *et al.*, 1975: 36, unless otherwise noted). *Catron Co.*: *Willow Creek, 10 mi. E Mogollon; Willow Creek area, 17.2 mi. E Mollogon; 20 mi. E Mogollon. Grant Co.*: *Mimbres Mts., Big Rocky Creek. McKinley Co.*: *Fort Wingate; Gallup; Cottonwood Gulch, 6 mi. S Thoreau. Valencia Co.*: *Porter's Ranch, 8 mi. SE Paxton* (Hooper, 1941:20).

## *Myotis evotis micronyx* Nelson and Goldman

1909. *Myotis micronyx* Nelson and Goldman, Proc. Biol. Soc. Washington, 22: 28.

*Type material.*—Adult male, skin and skull, USNM 146044; obtained on 8 November 1905 by E. W. Nelson and E. A. Goldman, original number 18490. Type locality Comondú, 700 feet, Baja California Sur. Type specimen not examined.

*Distribution.* —Known only from type locality (Fig. 7).

*Description.*—According to Nelson and Goldman (1909:28): "Much like *M. evotis*, but slightly smaller, with proportionately much smaller ears, thumb and claw; braincase more inflated anteriorly; free border of interfemoral membrane indistinctly ciliate as in *evotis*. Fur of upperparts, including middle of face, light golden cinnamon; sides of face thinly covered with dusky hairs; underparts gray, slightly tinged with buff. "

Measurements of the holotype (Nelson and Goldman, 1909:28) are: "total length, 90; tail vertebrae, 42; forearm, 35.8; tibia, 18.2; foot (dry skin), 7.9; thumb (dry skin), 5.7; height of ear (dry skin), 14.6. Skull: condylobasal length, 14.5; zygomatic breadth 14.3 [sic]; breadth of braincase, 7.2; depth of braincase, 5.3; maxillary toothrow, 6.2."

*Comparisons.*—This taxon is known only from the holotype, a male. According to Nelson and Goldman (1909:28): "skull is similar to *evotis*, but narrower; braincase higher, more inflated anteriorly, arching more abruptly from rostrum; palate narrower behind molars; bullae smaller. From that of *milleri* the skull differs in the same characters as *evotis*."

Comparisons presented here are based on published measurements of the holotype in the original description of *micronyx*, and include FA, CBL, BBC, DBC, and MTR. For differences between this and other pale-colored long-eared myotis from the western United States, *evotis, chrysonotus*, and *jonesorum*, see accounts of those subspecies.

From *M. e. milleri*, which is geographically nearest *micronyx*, this race differs as follows: larger externally (forearm of holotype 35.8, six male *milleri* averaged 34.2); cranium with slightly more inflated braincase than in *milleri*; skull larger (CBL of the holotype 14.5, four male *milleri* averaged 14.2); skull slightly deeper

5.3 (three male *milleri* averaged 4.9); MTR of holotype greater, measuring 6.2, whereas five male *milleri* averaged 5.8 (see Table 9).

From *M. e. pacificus* of the Pacific Northwest, this race is paler; size smaller (forearm of the holotype 35.8, average forearm in male *pacificus* is 36.3); CBL and BBC are about the same; DBC slightly greater; and MTR is shorter (6.2) than the average for male *pacificus* (6.4).

*Remarks.*—As previously mentioned, this bat is known from a single specimen. Using the published measurements as criteria, this specimen was classified with specimens from the Pacific Northwest (from which it differs as indicated above) by means of discriminant function analysis, and not with material from either southern California or northern Baja California. Inasmuch as nothing is known about variation or natural history of this bat, it is recommended that it be treated as a separate subspecies pending collection and analysis of additional data.

The published measurement for zygomatic breadth in the original description of this taxon is incorrect. At my request, D. E. Wilson kindly measured the specimen and reported the zygomatic breadth to be 9.3 not 14.3 as originally published.

### *Myotis evotis milleri* Elliot

1903. *Myotis milleri* Elliot, Field Columb. Mus., Publ. 74, Zool. Ser., 3:172.

*Type material.*— Adult male, skin and skull, Field Mus. Nat. Hist. 10840; obtained on 15 September 1902 by E. Heller, original no. not reported. Type locality La Grulla, San Pedro Mártir Mountains, Baja California Norte, México. Type specimen not examined.

*Distribution.*—Known only from vicinity of San Pedro Mártir Mountains, Baja California Norte, México (Fig. 7).

*Description.*—Smallest and palest of the races of *M. evotis*. External measurements are presented in Table 10. Cranial meaurements and color reflectance measurements are in Table 9. Average measurements for zygomatic breadth (not used in analyses) for four males (extremes), followed by the measurements of two females, are: 8.68 (8.48–887), 8.72, 8.78. Average weight of five males was 4.8 (4.0–5.4), whereas one female weighed 5.0.Reduker *et al.* (1983) reported the karyotype of *M. milleri* as having 2N=44 and FN=52, the same chromosomal arrangement (small biarmed autosome 23 and large Y chromosome) as reported by Bickham (1979) for *M. evotis*, *M. auriculus*, and *M. thysanodes*. Baker and Bickham (1980) considered these changes as shared derived characters.

*Comparisons.*—For comparisons with other pale-colored races, see accounts of *evotis*, *chrysonotus*, *jonesorum*, and *micronyx*. From *pacificus*, this bat differs in being much paler with marked contrast between pelage and patagia; size smaller externally (forearm less than, not more than, 36); cranium slightly smaller in all dimensions (see Tables 6 and 9).

*Remarks.*—Until my study, this bat has been treated as a separate species, *Myotis milleri*, because of its small size and, more recently, because of one fixed allelic difference (see Reduker *et al.*, 1983) between it and a sample of *M. evotis*. I treat it as a subspecies of *evotis* for the reasons outlined below.

It long has been recognized that there is a close evolutionary relationship between *Myotis evotis* and *M. milleri*. *Myotis* has a conservative karyotype and thus a relatively slow rate of karyotypic evolution, and related species differ by few or no chromosomal rearrangements (Baker and Bickham, 1980). The karyotype of *M. nigricans* was proposed as the standard for the genus, 2N=44 and FN=50, and was presumed "primitive" by Bickham (1979). Virtually all *Myotis* studied to date have a diploid number of 2N=44. The fundamental number, however, may be used to infer phylogentic relationships. Three species of North American long-eared Myotis (*evotis*, *thysanodes*, and *auriculus*) share the same fundamental number (FN =52) achieved by an heterochromatic addition to a short-armed chromosome (number 25), which represents a shared-derived condition. Additionally, in males of these three species the Y chromosome is large and made up mostly of heterochromatic material (Bickham, 1979; Baker and Bickham, 1980).

This same karyotypic pattern, 2N=44 and FN=52, with a large Y chromosome, has been reported for *M. milleri* as well (Reduker *et al.*, 1983). These authors stated (p. 675): "Morphologically, *M. milleri* is no more different from *M. evotis* in southern California (the closest *M. evotis* population known) than other *M. evotis* subspecies are from one another. Genetically, *M. evotis* and *M. milleri* posses a genic similarity value that is high (0.898) compared to those obtained from intraspecfic population comparisons. A fixed allelic difference at the ES-1 locus between these two taxa suggests that no introgression occurs between the two forms, however. Because no distinct cohesion is obvious between *M. milleri* and *M. evotis*, we feel that *M. milleri* should retain its specific status rather than be reduced to a subspecies of *M. evotis*."

Based on my morphological analyses, these bats are not significantly smaller than *evotis* of southern California and may, in fact, be the southern end of a clinal trend toward smaller size southward from Los Angeles and San Diego counties to northern Baja California. By way of example, two selected characters, one external and one cranial, vary in these three groups as follows (Los Angeles County, San Diego County, and northern Baja California): FA , 35.7, 35.4, 34.5; GLS, 15.6, 15.5, 15.3.

Avise (1975:465) suggested two points to consider when evaluating Roger's similarity coefficient for electrophoretic data: "(1) levels of genetic similarity between conspecific populations appear very high (populations nearly identical in allelic content at 85 percent or more of their loci) and (2) genic similarities between different, even very closely related species, are generally much lower and more

widely dispersed (congeneric species pairs often completely distinct at one-fifth to one-fourth of their loci)."

When considering genetic divergence below the species level, he (p. 469) further noted "the proportion of monomorphic loci ranges from 80 to 90% in most vertebrate populations."

Mean genic similarity (Roger's similarity) between *Myotis evotis* and three other species (two long-eared), *thysanodes*, *auriculus*, and *yumanensis*, were reported as 0.760, 0.768, and 0.753, respectively (Reduker *et al.*, 1983). These values are near those reported by others for closely related species of bats. For example, Baker *et al.* (1988) found the similarity ("genetic identity") between the sympatric *Lasiurus borealis* and *L. seminolus* to be 0.760, and between the former and two different populations of the allopatric *L. blossevillii* to be 0.801 and 0.845. The similarity level between the two populations (subspecies) of *blossevillii* was 0.946. Biochemical data reported for other lasiurines by Baker *et al.* (1988) are similar to those mentioned above. Genic differences of the same magnitude have been used to infer systematic relationships among other small mammals as well—see, for example, Block and Zimmerman (1991), on pocket gophers, Avise *et al.* (1979) and Calhoun *et al.* (1988) on *Peromyscus*, and George (1988) on *Sorex*.

In view of these data (that is, *milleri* not significantly different morphologically, from SOCAL, but correctly is classified in discriminant function analysis; karyotypes with identical diploid and fundamental number as well as same Y chromosome configuration; and Roger's similarity value of allozymes, 0.898), I suggest that *milleri* probably is best considered as a subspecies of *Myotis evotis*.

Specimens examined.—Total of eight as follows: Mexico. *Baja California*: La Grulla, Parque Nacional Sierra de San Pedro Mártir, 1 (MSB); *Sierra San Pedro Mártir, La Encantada* , 1 (MSB); *base of Picacho Piablo, Sierra San Pedro Mártir*, 1 (MSB); *1.0 mi. (by road) W Vallecitos, Sierra San Pedro Mártir*, 1 (MSB); *15 km S Vallecitos, entrance to Parque de Nacional, Sierra San Pedro Mártir*, 2 (MSB); *Vallecitos, San Pedro Mártir*, 2 (MSB).

### *Myotis evotis pacificus* Dalquest

1943. *Myotis evotis pacificus* Dalquest, Proc. Biol. Soc. Washington, 56:2.

*Type material*.—Adult male, skin and skull, Mus. Vert. Zool. 94173; obtained on 3 August 1940 by John Chattin, original no. 620. The type locality was designated by Dalquest (1943) as 5 mi. N, 3.5 mi. E Yacolt, 500 ft., Clark Co., Washington. Type specimen not examined.

*Distribution*.—Southern and western British Columbia, Washington, western and northern Oregon, coastal areas of northwestern California, northern Idaho, and northwestern Montana (Fig. 7).

*Description*.—A small race of the long-eared myotis characterized by dark pelage and heavily pigmented ears and membranes. Pelage of middorsal region approximately 8 to10 in length, the distal 3 to 4 of each hair with rich brownish-blackish color (not golden as in other subspecies), hairs black basally. Forearm

moderately short for the species (approximately 35.6 to 37.2), greatest length of skull ranging from about 15.4 to 15.6. This taxon frequently is taken at lower elevations than are other subspecies. External measurements given by Dalquest (1943) for the type specimen and four topotypes averaged: total length, 85; length of tail, 41; length of hind foot, 7.4; length of ear, 19.4;weight 5.5 grams. Representative external measurements are given in Table 10; length of forearm, cranial measurements and color reflectance readings for pelage are presented in Table 6.

Averages for zygomatic breadth (not used in analyses) of 18 males and 23 females (extremes in parentheses) from this sample (Group 1, PACNW) was 9.2 (8.9–9.4) and 9.1 (8.4–9.7), respectively. Average weight of 12 males and 22 females from this sample was 5.2 (4.0–7.0) and 5.3 (4.0–7.2), respectively.

*Comparisons.—Myotis evotis pacificus* is the darkest subspecies of the species, significantly different from others, and is the only race that can be identified reliably to subspecies on the basis of pelage color alone. Other known races must be separated using mensural data (for example, length of forearm and greatest length of skull). For comparisons with other subspecies, see the previous accounts and Tables 6, 9, and 10.

*Remarks.*—My examination of specimens clearly shows that the *M. evotis* with the darkest pelage occurs on the western slope of the Cascade Mountains of Oregon and Washington. Farther inland, bats are dark in color but not quite as heavily pigmented as are coastal representatives; however, they are certainly much more darkly pigmented than individuals of the pale-colored races *chrysonotus* and *evotis*. I found it somewhat difficult to assign to subspecies seven specimens from northwestern Montana (four from Flathead County and three from Missoula County). These seven show pelage characteristics of *pacificus* (percent reflectance red averaged 13.2 and 13.3, respectively), but in size they approach the inland race *chrysonotus* (length of forearm, 38.6 and 38.3, and greatest length of skull, 15.8 and 15.9, respectively). They are here assigned to *pacificus* on the basis of pelage color, but clearly represent an intergrading population. A single specimen from Shuswap, British Columbia, shows similar tendencies (length of forearm, 37.4; greatest length of skull, 16.1; and percent reflectance red, 11.5). Likewise this specimen is referred to *pacificus*.

Miller and Allen (1928) referred specimens from the Blue Mountains, southeastern Washington, to *pacificus* as now understood, but, Dalquest (1958) disagreed and assigned them (only four were available to him at that time) to the "pale race." Bailey (1936:373) reported that these specimens were "mainly intermediate" and referred them to the coastal race. I have examined specimens from this region, and others from the south in Oregon and here refer all to *pacificus*. They are, in fact, slightly paler on average than specimens from coastal areas of Washington and Oregon, but not nearly as pale as interior races such as *chrysonotus*.

In Idaho, these bats are known certainly only from in the west-central part of the state (Adams County). Few records are known from the region. One specimen available to me had the following measurements: length of forearm, 37.2; greatest length of skull, 15.5; and percent reflectance red, 12.5. These indicate *pacificus* rather than *chrysonotus*.

*Specimens examined.*—Total of 167 as follows. British Columbia. Shuswap,1 (USNM). California. *Humboldt Co.*: *8 mi. N, 1.5 mi. E Arcata*, 1 (MSB); Schoolhouse Peak, 2 (MVZ); 20 mi. E Korbel, 1 (HSU). *Mendicino Co.*: 7 mi. S, 3.6 mi. E Ukiak, 2 (MVZ). *Siskiyou Co.*: Mount Shasta, 2 (MVZ). *Sonoma Co.*: 1.75 mi. SE Guerneville, Mays Canyon, 1 (MVZ). *Trinity Co.*: *White Rock Ranger Station*,1 (MVZ); Divide, 12 mi. N Yolla Bolly Mt., 1 (MVZ); South Yolla Bolly Mountain,1 (USNM). Idaho. *Adams Co.*: *Tamarack*,1 (USNM); Summit Smith Mtns., 1 (KU). Montana. *Flathead Co.*: Glacier National Park, 1 (UMZ); Glacier National Park, Camas Creek, 1 (UMZ); *1 mi. above Camas Creek Bridge, Glacier National Park*, 1 (UMZ); *3 mi. above Camas Creek Bridge, Glacier National Park*, 1 (UMZ); *1 mi. E Camas Creek, Glacier National Park*, 1 (UMZ); *2 mi. E Camas Creek, Glacier National Park*, 1 (UMZ). *Lake Co.*: Flathead Lake, 1 (UMZ); Flathead Lake, Biological Station, Yellowbag, 1 (UMZ). *Missoula Co.*: Missoula, 1 (UMZ); *Pattee Canyon*, 2 (UMZ); *O'Brice Creek*, 1 (UMZ). Oregon. *Baker Co.*: East Piner Creek, 2.5 mi. NE Cornucopia, 1 (USNM). *Benton Co.*: *1.5 mi. NW Wier*, 1 (PSMNH); *11 mi. S Corvallis, W. L. Findley Wildlife Refuge*, 1 (PSMNH); 9 mi. E Alesa, 5 (MSB); *4.5 mi. N Corvallis*, 3 (OSUFW); *1.5 mi. N Corvallis*, 3 (OSUFW); Corvallis, 1 (OSUFW). *Clackamas Co.*: Molalla, 1 (PSMNH). *Clatsop Co.*: 1 mi. W Hamlet, 4 (PSMNH). *Coos Co.*: 4 mi. SE Bunday, 1 (PSMNH). *Deschutes Co.*: *Sparks Lake*, 1 (MVZ); Sisters, 1 (USNM); *Indian Ford*, 1 (OSUFW). *Grant Co.*: Cold Springs, 8 mi. E Austin, 1 (MVZ). *Klamath Co.*: Oregon Caves, Carter Lake National Park, 1 (USNM), 1 (MVZ); *Royston Spring*, 1 (PSMNH). *Klamath Co.*: Rainbow Creek, 2 mi. SE Lake of the Woods, 1 (MVZ); *National Park Headquaters, Crater Lake National Park*, 1 (MVZ). *Lane Co.*: O'Leary Peak, 10 mi. S McKenzie Bridge, 1 (USNM). *Lincoln Co.*: Cascade Experimental Forest, 13 (PSMNH); Yaquina, 5 mi. E Newport, 1 (OSUFW). *Tillamook Co.*: Tillamook, 1 (PSMNH), 1 (OSUFW); *Pleasant Valley, 9 mi. SE Tillamook*, 2 (OSUFW); *Cape Meares*, 1 (OSUFW). *Wallowa Co.*: Rockwall Springs, 11.5 mi. NNE Wallowa, 29 (PSMNH); *9.5 mi. NNE Wallowa* , 9 (PSMNH). *Wheeler Co.*: 7 mi. S, 11 mi. W Mitchell , 1 (MVZ). *Union Co.*: Starkey Experimental Forest, 17 (PSMNH); *Dinner Bucket Pond, Starkey Experimental Forest*, 3 (PSMNH); *9 mi. NW LaGrande*, 2 (PSMNH); *LaGrande*, 1 (PSMNH). Washington. *Clallam Co.*: Elwha River, 7 (PSMNH); *Lower Elwha River*, 1 (PSMNH). *Clark Co.*: Battle Ground , 1 (KU); *5 mi. N, 3.5 mi. E Yacolt*, 2 (MVZ). *Columbia Co.*: Blue Mountains, 1 (WSM); *Mountain Top*, 2 (WSM); *Blue Mountains*, 6 (WSU-Seattle); Blue Mountains, 1 (MVZ); *Stayawhile Spring*, 1 (MVZ). *Douglas Co.*: Douglas Creek, 11 mi. S, 8 mi. E Waterville, 1 (BM-WSM). *Grays Harbor Co.*: 5 mi. W Lake Quinault near Hwy. 101, 1 (PSMNH). *Pend Oreille Co.*: 1 mi. N, 3 mi. E Blueside, Le Clerc Creek, 1 (BM-WSM). *Pierce Co.*: *Parkland [Parkway]*, 1 (PSMNH); Mount Rainier National Park, 1 (PSMNH). *Kittitas Co.*: Easton, 1 (USNM).

*Selected additional records.*—British Columbia (records from Cowan and Guiguet, 1960:82, unless otherwise noted): Kimsquit; Kingcome Inlet; Parksville (van Zyll de Jong, 1985:98); Victoria; Hope; Allison Pass (Manning Park). Washington. *Columbia Co.*: Godman Springs (Dalquest, 1948:153); Godman Springs (Miller and Allen, 1928:116). *Walla Walla Co.*: *South Touchet* (Miller and Allen, 1928:116).

## Evolutionary Relationships of North American Long-Eared Myotis

The evolutionary relationships of North American long-eared myotis—the species *auriculus*, *evotis*, *keenii*, *septentrionalis*, and *thysanodes*—have been addressed in the past by a number of mammalogists, notably by Miller and Allen (1928), Dalquest (1943), Baker and Stains (1955), Hoffmeister and Krutzsch (1955), Findley (1960; 1972), Genoways and Jones (1969), Bickham (1979), van Zyll de Jong (1979), Baker and Bickham (1980), and Reduker *et al.* (1983), each contributing to what we now know about these bats. Still, there is much to be learned about long-eared myotis.

*Fossil record.*—Known fossil material referable to *M. evotis* is limited and is Holocene to late Pleistocene in age (Kurtén and Anderson, 1980). Remains have been recoverd from deposits in Schulze Cave, Edwards Co., Texas (Dalquest *et al.*, 1969), Klein Cave, Kerr Co., Texas (Roth, 1972), Little Box Elder Cave, Converse Co., Wyoming (Anderson, 1968), and Papago Springs Cave, Santa Cruz Co., Arizona (Skinner, 1942). The long-eared myotis is not currently known to occur in Texas; therefore, the past presence of this species at that latitude no doubt indicates a cooler, moister climate there in late Pleistocene times. According to Kurtén and Anderson (1980), *keenii* [=*septentrionalis*] is known from late Pleistocene and subRecent material as follows: Bootlegger Sink, Pennsylvania; Natural Chimney, Virginia; New Paris no. 4, Pennsylvania; Robinson Cave, Tennessee; and Organ-Hedrick Cave, West Virginia. Fossil material of late Pleistocene age referable to *thysanodes* has been found in Little Box Elder Cave, Wyoming, Papago Springs Cave, Arizona, and Isleta Cave, New Mexico.

*Taxonomy.*—*Myotis evotis* traditionally has been classified as a member of the *evotis* group of the subgenus *Myotis*, whereas *M. thysanodes* has been relegated to the *nattereri* group of that same subgenus (Findley, 1972). Corbet and Hill (1991) listed *auriculus*, *evotis* (and *milleri*), *keenii*, and *septentrionalis* as belonging to the subgenus *Paramyotis* (along with *M. bechsteinii* of the Old World), placing *M. thysanodes* as the only American member of the subgenus *Isotus*, which also includes three Old World species (*bombinus*, *nattereri*, and *schaubi*) with a distinct uropatagial fringe. This subgeneric classification does not jibe, however, with karyotypic data, because the species *auriculus*, *evotis*, and *thysanodes*, the only known American myotis with a fundamental chromosome number of 52, "appear to be karyotypically derived" (Bickham, 1979:796). Furthermore, they are "considered closely related and members of the monophyletic group of 'long-eared' species (subgenus *Myotis*)" based on chromosomal, morphologic, and electrophoretic data (Bickham *et al.*, 1986:749).

Menu (1987) suggested the use of *Leuconoe* Boie, 1830 as the generic name for North American myotis, replacing *Myotis* Kaup, 1829, which he regarded as a sub-

genus. Clearly the earlier name has priority. I follow Corbet and Hill (1991) and others in the use of the generic name *Myotis*.

*Morphology of teeth.*—Insectivorous bats have essentially primitive tribosphenic dentition of the dilambodont type. Upper molars have a hypocone and basal lingual cingula, whereas lower molars have a labial cingula. There is a tendency to lose the metacone from the last upper molar (Slaughter, 1970).

Bat teeth vary in size relative to the size of the bat. Large species like *M. thysanodes* appear to be large-toothed when compared to a smaller species such as *M. septentrionalis*, which appears to be small-toothed even to the unaided eye. In American long-eared myotis, both upper and lower incisors and canines vary little between species except in relative size, nor do lower premolars and molars show distinctive species-specific traits. It is noteworthy, however, that no American *Myotis* has the second triangle of m3 so much reduced as in the Palearctic *M. myotis* (Miller and Allen, 1928).

Upper premolars may be helpful as a aid in identification based on their relative position in the toothrow. For example, the first two premolars in *M. thysanodes* frequently are crowded inward, especially P3. Slight inward crowding, not nearly as marked as in *thysanodes*, of P3 occurs in two other long-eared species, *auriculus* and *evotis*. No inward crowding of premolars was detected in *keenii* or *septentrionalis*.

The first and second upper molars are most useful in distinguishing among long-eared taxa and evaluating evolutionary relationships. The assumed "primitive" or ancestral condition of these teeth, as seen in most North American members of the genus, has four major cusps—protocone, paracone, metacone, and hypocone, plus well-developed accessory cusps and lophs, protoconule, paraloph, and metaloph. Loss or reduction of these accessory cusps and lophs is considered a derived condition. All long-eared bats show some tendency toward reduction of accessory cusps and lophs, especially when compared with *Myotis lucifugus* (Fig. 8A). This trend was alluded to by Miller and Allen (1928:125), who noted that in the reduced condition of secondary cusps and ridges of M1 and M2 "*M. thysanodes* shows the culmination of a series of changes whose earlier stages are seen in *M. keenii* and whose development may be traced in *M. evotis*" (Fig. 8 B-F).

*Comparisons.*—In the following discussion, pairs of species will be treated together and then compared with other long-eared bats. Based on karyotypic evidence and morphology, especially of the teeth, the least derived species among North American long-eared taxa, *M. keenii* and *M. septentrionalis*, are treated first, followed by the intermediate species *M. auriculus* and *M. evotis*, and finally *M. thysanodes*, presumably the most derived.

Though long suspected as representing two species (Fitch and Shump, 1979), only recently have the allopatric taxa *keenii* and *septentrionalis* been recognized as specifically distinct (van Zyll de Jong, 1979). These bats share a number of traits

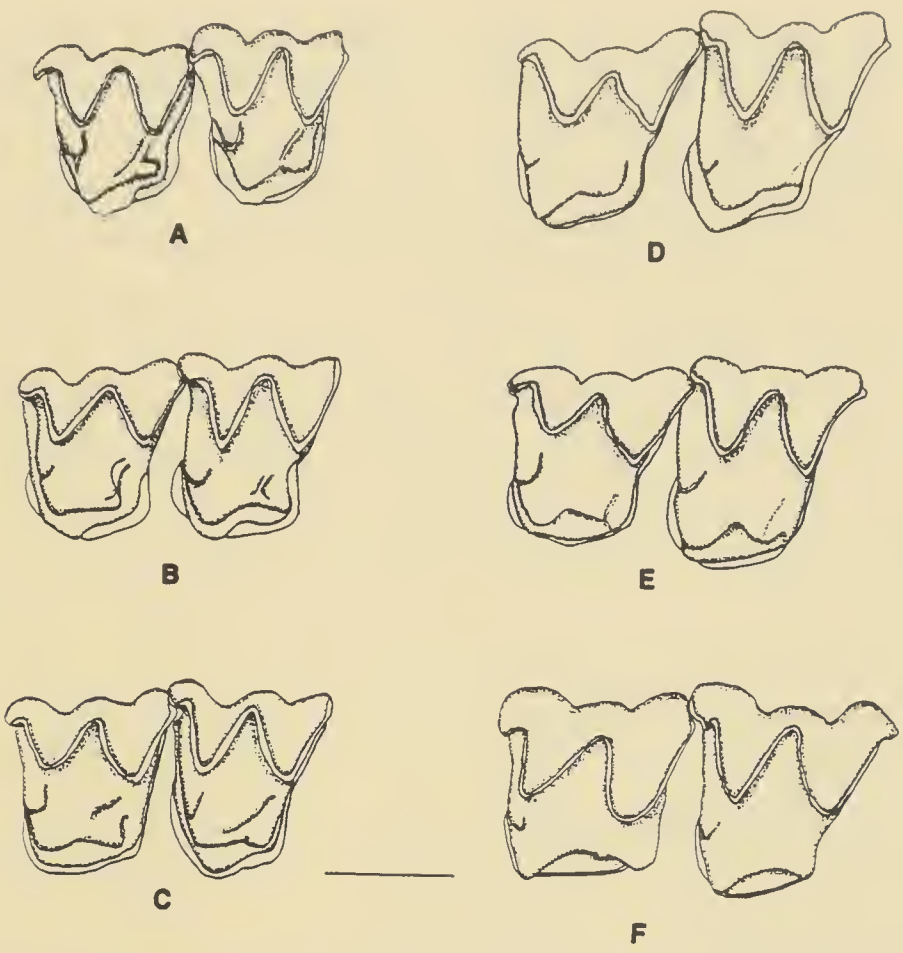



FIG. 8.—Occlusal view, to scale (bar at bottom equals 1 mm) of first and second upper left molars from six species of *Myotis*: A, adult male *Myotis lucifugus* (TTU 23032) from Marion County, Iowa; B, adult female *M. keenii* (BM-WSU 34206) from Island County, Washington; C, adult male *M. septentrionalis* (TTU 23023) from Jones County, Iowa; D, adult male *M. evotis* (TTU 60270) from Socorro County, New Mexico; E, adult male *M. auriculus* (TTU 10923) from Tamaulipas, México; and F, adult male *Myotis thysanodes* (TTU 11493) from Cochise County,

that differ from those in other long-eared species here considered including the following: primitive karyotype (see remarks beyond); skull and especially auditory bullae small; upper first and second molars with primitive accessory cusps, paraloph, and metaloph; sagittal crest lacking; upper premolars usually in line with molars.

*Myotis keenii* is slightly smaller than *M. septentrionalis* according to van Zyll de Jong (1979). He listed four (one external, three cranial) univariate characters that best discriminate between these two taxa (averages in millimeters, for a sample of *keenii* followed by averages for two populations of *septentrionalis*): length of ear, 18.3, 17.2, 16.2; basal width of upper canines at cingulum, 0.72, 0.80, 0.81; width across upper incisors, 2.44, 2.66, 2.65; and width of rostrum just posterior to canines, 3.32, 3.63, and 3.57. He found no significant differences in length of forearm, greatest length of skull, length of P4-M3, or length of M2.

*Myotis evotis* and *Myotis auriculus* are morphologically similar as demonstrated in previous studies—see Findley (1972) and Reduker *et al.* (1983). The latter authors reported overlap in cranial dimensions between these two species except in the San Mateo Mountains of New Mexico, where they occur sympatrically and

where *M. evotis* is noticeably the larger, evidently a classic example of character displacement. They also noted the morphological distinctness of *thysanodes* from *auriculus* and *evotis*. At different times, until its recognition as a distinct species (Genoways and Jones, 1969), *Myotis auriculus* once was classified as a subspecies of either *evotis* or *keenii* (Hoffmeister and Krutzch, 1955; Baker and Stains, 1955; Findley, 1960). Both of these bats, *evotis* and *auriculus*, share a number of traits that separate them from *keenii* and *septentrionalis*, including: derived karyotype (see remarks beyond); skull medium to large in size: auditory bullae relatively large; upper first and second molars with intermediate condition of accessory cusp with paraloph and metaloph reduced but usually present; sagittal crest present at least in some individuals, but never pronounced; upper premolars usually in line with molars, but slightly crowded inward in some individuals. Reduker *et al.* (1983: 674-675) attributed morphological similarity of *auriculus* to *evotis* as a retention of "primitive morphological character states" possibly due to "similar types of foraging modalities."

*Myotis auriculus* differs from *evotis* as follows: ears brownish rather than blackish, usually shorter than 21; dorsal hairs brown basally rather than black; uropatagium lacking fringe of hairs; cranium more inflated anteriorly; median postpalatal process long, broad, and rounded, not short and pointed; dentary relatively longer, more than 82.5 percent of condylobasal length (Findley, 1960; Genoways and Jones, 1969; Warner, 1982).

The fringed myotis, *Myotis thysanodes*, is one of the largest North American members of the genus. This bat has a well-developed fringe of stiff hairs on the posterior margin of the uropatagium; derived karyotype (see remarks beyond); skull medium to large in size; auditory bullae relatively large; metaloph absent from first and second upper molars, accessory cusp and paraloph usually reduced and frequently absent; sagittal crest usually well developed; upper premolars frequently crowded inward (O'Farrell and Studier, 1980). Reduker *et al.* (1983:675) speculated that "this morphological uniqueness is a reflection of the acquisition of a unique type of foraging strategy or niche exploitation."

*Karyology.*—Among *Myotis* worldwide, the known diploid number of chromosomes is 44 except in one case of 46 (the Asian *M. annectans*—Bickham *et al.*, 1986) and the fundamental number ranges from 50 to 56 (McBee *et al.*, 1986). All American species have 2N=44; all have FN=50 except the three long-eared taxa, *M. auriculus*, *M. evotis*, and *M. thysanodes*, which have the derived condition of FN=52. *M. septentrionalis* (and presumably *keenii*) have the proposed ancestal condition of 2N=44, FN=50. The differences in fundamental number among species of *Myotis* is mostly the result of presence or absence of heterochromatic short arms on smaller autosomes (Bickham *et al.*, 1986), which are considered derived characters. In the case of the three American species with FN=52, the in-

creased fundamental number derives from a metacentric (rather than acrocentric) condition of autosome 25.

*Genic data.*—Reduker *et al.* (1983) studied five species of *Myotis* from the southwestern United States, *yumanensis*, *auriculus*, *evotis*, *thysanodes*, and the then distinct *milleri*. Their cladistic analyses of electrophoretic mobility of allozymes (20 presumed loci, 12 of which were monomorphic) suggested that *M. thysanodes* shared a common ancestor with *M. evotis* after the divergence of *M. auriculus*, a conclusion at variance with some other data. These authors presented a phenogram produced by clustering of Roger's similarity values in which *auriculus* clustered with *yumanensis*. Their study did not, however, include two other North American long-eared species, *keenii* and *septentrionalis*, or any representatives of long-eared myotis from the Old World.

*Historical biogeography and evolution.*—An evolutionary relationship has been hypothesized between North American long-eared myotis *M. evotis*, *M. keenii*, and *M. thysanodes*, and the Old World *M. nattereri*, *M. emarginatus*, and their relatives (Miller and Allen,1928; Findley, 1972). Findley (1972:45) concluded that *Myotis* "originated in warm temperate and tropical parts of the Old World, probably in the Oriental Region rather than Africa, since the latter continent is rather depauperate from the standpoint of myotine diversity." If we accept Findley's hypothesis, which seems reasonable, then it is easy to imagine emigration of some species to North America, by way of Beringia, during the mid-to-late Tertiary. It is equally reasonable to believe that populations of long-eared bats subsequently were displaced southward by recurring shields of glacial ice that covered much of northern North American during the Quaternary. Southward shift of populations and their subsequent disjunction into isolated units allowed time for each to evolve independently. Upon recession of glacial ice and subsequent northward movements of populations, the groups remained distinct and mostly allopatric (for example, *keenii* and *septentrionalis*). Both allopatry over most of their distribution and habitat separation where they occur together—*auriculus* at lower elevations and *evotis* at higher elevations—may be isolating mechanisms involved in maintaining distinct present-day populations.

It is unclear whether all North American long-eared myotis are monophyletic or are descendants from two or more ancestral migrants from the Old World. The latter situation seems most parsimonius, particularly if lineages with different chromosomal characteristics are represented. However, "it is possible that the biarmed condition of pair 25 has evolved more than once among the North American species" (Bickham *et al.*, 1986:749).

Based on karyotypes (FN=50) and cranial and dental morpholgy, two North American long-eared species represent the basal group among these bats—the sister taxa *keenii* and *septentrionalis*, with northern and eastern distributions. Three species (FN=52), the sister taxa *evotis* and *auriculus*, with southern and

western distributions, and *M. thysanodes*, with a widespread distribution in western North America, clearly are derived taxa. American long-eared bats of the genus *Myotis* probably represent the descendants of two independent invasions from the Old World, but this problem of relationships cannot be resolved until all members of the genus *Myotis*, or at least the Palearctic representatives, are analyzed in more detail, using additional data sets.

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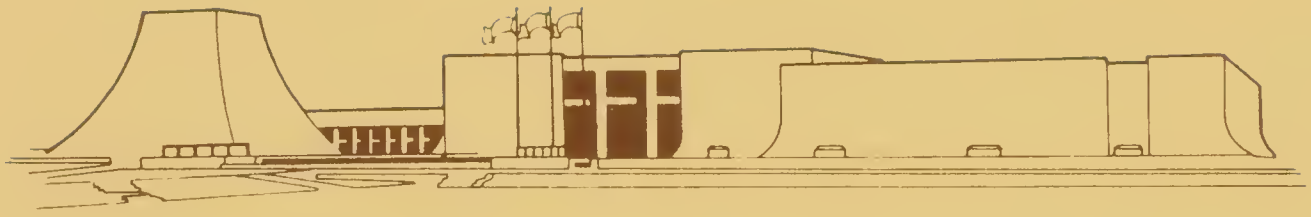

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